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EPIGENESIS OR EVOLUTION.

“DES Sages appelés à éclairer la Monde ont choqué les règles de la logique la plus commune. Ils ont jugé du tems ou les parties d'un animal ont commencé d'exister par celui ou elles sont commencé à devenir visibles ; et tout ce qu'ils ne voyaient point, n'existait point.”

These words, written by Bonnet nearly a century and a quarter ago, are expressive of the belief in the evolutionary theory of development, then universally accepted in spite of the labours of Harvey and C. F. Wolff. This evolutionary doctrine, after being thoroughly discredited by the labours of the embryologists of the last fifty years, is now with us again, not perhaps in its old form, the evolutionists of to-day are anxious to repudiate that, but in a form which differs from the old one only because of the more numerous accumulation of facts and observed sequences which the theory is called upon to explain.

The evolution doctrine in its earliest phases was crude enough: An animal was supposed to pre-exist fully formed and complete within the egg, but as a miniature, generally so small as to be unrecognisable by the eye, even when aided by the best optical instruments then in use. This somewhat singular view was founded chiefly on a supposed observation of Malpighi, who had affirmed that he had seen the body of the chick in the egg at the time at which it was laid and before it had been incubated. The observa-

tions of Swammerdam on the development of the frog tended to confirm this view, but it is evident, from a perusal of Swammerdam's work and a study of his drawings, that he must have been strongly predisposed in favour of the evolution theory and have deceived himself in looking for the "præformatio," which he figures, though nothing like it exists.

This pre-existent miniature of the future animal was supposed to nourish itself and grow, not in the way that we now understand the process, but by taking in ready-made material particles and packing them amongst the particles of its own body, which was thereby caused to expand, unfold and develop, just as gelatine is caused to swell up when soaked in water. The pre-existent germ, it was supposed, was stimulated to this course of development by fecundation, by which process its latent or potential activities were awakened, a conception which has been nearly faithfully repeated within the last eighteen months.¹

It must not be thought, however, that the evolutionists of the eighteenth century were by any means unanimous in accepting so very crude a theory. As physical and chemical phenomena came to be better understood, so was this theory seen to be more and more unsatisfactory, and Bonnet, who accepted it with all its consequences in his earlier years, was led in his later writings to make very considerable modifications in his views. He no longer regarded the germ as an organised body reduced to miniature, but as "an original preformation from which, as from its immediate principle, an organic whole may be produced". The conception of a pre-existing entity in the germ, as thus expressed, is not very different from the *primordium vegetale* of Harvey, and, if allowance be made for the great difference that there is between the knowledge of the minute structure of animal tissues of to-day and that of a hundred years ago, it bears

¹ Durch die Befruchtung werden also nach meinen Auffassung zunächst kinetische Energieen der direkten Entwicklung produziert oder ausgelöst. W. Roux, Beiträge zur Entwicklungsmechanik des Embryo (*Referate ü Beiträge zur Anatomie und Entwicklungsgeschichte, Bonnet and Merkel, Anat. Hefte*, bd. ii., p. 293).

a tolerably strong resemblance to some of the most recent theories that have been put forward.

In estimating the value of the doctrines of the older biologists this fact should not be lost sight of, that for want of good microscopes and of proper methods of microscopical investigation, they were very far from having those clear and definite conceptions of minute structure which we now possess. The conclusions to which they arrived may have been, indeed they often were, very ingenious and acute, but the want of definite ideas of cell structure and cell division, and, above all, the want of a sufficient number of instances taken from all parts of the animal kingdom, is apt to lead us to underestimate the value of their generalisations when compared with the very similar results obtained in the present day. It is certainly a striking fact that the most minute and elaborate researches of the last few years have led the course of biological speculation back to the point of view of Haller and Bonnet in the eighteenth century, and have threatened to discredit altogether the opposite doctrine of epigenesis, which, as the result of the cell theory of Schleiden and Schwann, and the accumulated work of embryologists from the time of Von Bär and Rathke onwards, seemed to be triumphant all along the line.

The doctrine of epigenesis, really due to Aristotle, but elaborated and definitely propounded by Harvey, is simply a statement of the observed and observable facts in the ontogeny of any multicellular organism. In the egg, whatever may be its shape in its mature condition, one cannot, by any optical aid or chemical methods, recognise any structure more complex than that which is characteristic of a simple cell. This is an incontrovertible fact which has over and over again been insisted upon, and in spite of the recent additions to our knowledge of cell structure, the same statement which was made, and more than once repeated in Balfour's *Embryology*, holds as good to-day as it did ten years ago, namely, "that the ovum in its young condition is obviously nothing but a simple cell, and such it remains till the period when it attains to maturity". The circumstance that we are now able to recognise in the ovum several

varieties of protoplasm, that we generally acknowledge the chromatin substance of the nucleus to have some special effect in determining the mode of cleavage, and that we have a far more exact knowledge of the phenomena displayed by the nucleus during maturation, fecundation, and division than we had at the time when Balfour wrote, does not in any degree invalidate the above statement. The extrusion of the polar bodies and the fusion of the male and female pronuclei are indeed phenomena which are peculiar to the germ cell; but when the fusion has taken place, all that may be predicated of the oosperm may with equal force be predicated of any other cell in the organism. As the result of impregnation we do not see an altered ovum nor an altered nucleus. We know that, in fact, the ovum has got rid of part of its nuclear substance by the extrusion of the polar bodies, and that the portion thus lost has been made up by the union of the male pronucleus with the remainder of the egg nucleus. We infer that an important conjunction of material has been effected, and the subsequent history of the oosperm and a consideration of the facts of heredity forces us to the conclusion that the union of these minute particles of matter has, in fact, been of the utmost importance; but further than this we cannot go with certainty; all beyond is conjecture which has a greater or less amount of probability, according as it enables us to explain, in a reasonable and logical way, a greater or less number of observed facts and sequences. The subsequent history of the oosperm, that is of the ovum after it is impregnated, is an absolute demonstration of epigenesis in the sense in which it was understood by Harvey and by Caspar Friederich Wolff. It is, as has been aptly said by Herbert Spencer, a progression from the simple and homogeneous to the complex and heterogeneous; there is no unfolding of parts already existent, but a successive formation of new parts, which were not previously existent *as parts*. This is a point which must be insisted upon; it was insisted upon clearly and distinctly by Wolff in his *Theoria Generationis*, and his argument stands unshaken to-day as it did when he first wrote it. Epigenesis is a

statement of morphological fact ; it is not, and does not pretend to be, an explanation of those facts. There may be, in all probability there is, we may even go so far as to say with Weismann that there *must* be, some great complexity of matter underlying those gross and sensible form changes which are all that the best powers of our microscopes can make evident to our senses, but that is an inference which we are at present unable to verify. Tissues, organs, structures which can be apprehended by our senses, and demonstrated, are not present as such in the ovum ; they are gradually and successively established in the course of ontogeny, "*Alias post alias natas, ordine quasque suo emergentes,*" just as Harvey wrote of them in the seventeenth century.

Those who now contend for an evolutionary theory of development, as the only possible mode of explaining the facts of heredity, occupy the same position towards the doctrine of epigenesis as Wolff occupied with respect to Bonnet. The argument in both cases is the same : you cannot see these miniature structures, says Bonnet, what right have you to say, therefore, that they do not exist? The answer of Wolff is clear and philosophical : "Omnino, quidquid sensibus non patet, quod ideo non existat, absolute non potest affirmari. Interim vero plus elegantiae quam veritatis hoc principium habet, ad hæc experimenta applicatum. Partes constitutivæ, ex quibus omnes corporis animalis partes in primis initiis componuntur sunt globuli, mediocri microscopio cedentes semper. Quis autem diceret, se non potuisse corpus videre propter exiguitatem, cujus tamen particulæ constituentes propter exiguitatem ipsum fugere nescirent? Nemo unquam efficacioris lentis ope partes detexit quas non statim vilioris notæ microscopio deprehenderit. Aut enim nullo modo deprehenduntur, aut satis magnæ apparent. Absconditæ igitur partes propter infinitam parvitatem, indeque emergentes, fabulæ sunt . . . et tandem quando incipiant vasa existere, et quomodo incipiant ad oculum demonstrabo."¹

¹ C. F. Wolff, *Theoria Generationis*, ed. Nov. Aucta et emendata, 1777, p. 94.

The demonstration, remarkably complete when the conditions of work are considered, follows. It appears to me, though it may be a reactionary view to take, that for morphologists, who professedly make a study of *form*, the doctrine that "parts which are hidden because of their infinite smallness, and gradually emerge from it, are fables," is an extremely wholesome one. I do not wish to be misunderstood in this matter. The various "gemmules," "plastidules," "micellæ," "inotagmata," "plasms," "biophors," the whole company of assumed existences demanded for the theoretical explanation of observed facts, has been no doubt extremely useful in its proper place, and has done much to stimulate inquiry and give precision and definite direction to research. But we should remember always that they are, one and all of them, *fabulæ*; they are not sensible existences, and they have not even the value of the analogous assumptions, atoms and molecules, because, unlike these last, they cannot be made serviceable for calculations, they cannot be put to the test of a rigorous logical method. There is a time and a place for all things, for scientific speculation and for statement of scientific fact; it seems to me that speculation is out of place when the existences which it assumes are incorporated into statements of fact, and when the course of events which it has pictured is held to have overthrown a doctrine so firmly and satisfactorily founded on fact as that of epigenesis.

I am not raising a ghost for the purpose of laying it. Weismann, who began by seeking for an epigenetic theory of development, has altogether given up the attempt in his last work, and he states frankly that he is an exponent of an evolutionary doctrine. Thus, "Spencer's theory is epigenetic, Darwin's evolutionary; in this respect the latter is, in my opinion, superior to the former".¹

¹ The Germ Plasm, a theory of Heredity by August Weismann, translated by W. Newton Parker and Harriet Rönnefeldt. London: W. Scott, Limited, 1893, p. 5.

Wilhelm Roux is no less positive: "Das Ei schon von vornherein aus entsprechend vielen verschiedenen Teilen zusammengesetzt sein muss, dass die Entwicklung, also wesentlich Metamorphose von Mannigfaltigkeit, Evolution in unserem Sinne ist, trotz, der formalen Epigenesis C. F. Wolff's".¹ Roux, however, seems to be inconsistent in describing the evolutionary product, the cell aggregate, as a "mosaic work," an inconsistency to which I shall have occasion to refer later on.

Finally, we have the opinion of C. O. Whitman, who in a very able paper² calls into question the whole cell doctrine, and gives his adherence to the evolutionary theory in the most unmistakable manner. He says "that organisation precedes cell formation and regulates it, rather than the reverse, is a conclusion that forces itself upon us from many sides".

I am not going to accuse any of these authors, who are far too acute to fall into such an error, of confusing the issue between epigenesis and evolution to the extent which might appear from these quotations. Epigenesis, as Roux states, is a *formal* statement of the observed facts of ontogeny. It has been pressed into the service of speculation, and attempts have been made, we shall see shortly that they still are being made, to form an epigenetic theory to explain the causes of heredity. It is likely enough that these attempts have been hitherto failures; but the fact that the imaginary and theoretical superstructure has proved to be flimsy does not in the least affect the solidity of the building, on which the superstructure was, in truth, a mere excrescence. There is some reason to fear that, unless a protest is raised, the failure of the attempts to form hypotheses explaining the causes of developmental phenomena on epigenetic grounds, will discredit the doctrine of epigenesis as a statement of the observed facts of development. Weis-

¹ W. Roux, *loc. cit.*, p. 284.

² C. O. Whitman, "The Inadequacy of the Cell Theory," *Journal of Morphology*, vol. viii., August, 1893.

mann, for one, has thoroughly understood the distinction,¹ but as he is more concerned with the establishment of his own evolutionary *theory* than with the definition and limitation of epigenesis *as a statement of observed fact*, there is danger that the passages in which he makes the distinction will be overlooked, and that his deservedly great authority will be made use of by those who wish to relegate epigenesis to the *limbus fatuorum*. There must be no mistake, epigenesis is a fact, not a theory; it is only when we attempt to analyse the phenomena of development still further, to go behind the appearances which are familiar to all those who have ever studied the embryology of a few multicellular organisms, and to seek for some explanation of appearances and sequences of which we recognise the form but do not understand the essence, that we are thrown back on a theory which in some measure resembles that of the physiologists of the eighteenth century. Bonnet was perfectly right when he cast ridicule upon those who asserted that things which could not be seen could not therefore exist. This is admitted at once by Wolff in the passage quoted above, but Wolff was not without reason when he said that this principle had more elegance than truth in it, when applied to the phenomena under consideration. The existence of material particles having form and figure, which are nevertheless beyond the ken of our vision, even when aided by the very best microscopes, can neither be affirmed nor denied by the morphologist. That there are such things as ultimate vital units of which many millions may be re-

¹ "If, however, the id has a right and left half in bilateral animals, we must not thereby infer that it is merely a miniature of the fully formed animal, and that therefore we are once more dealing with the old theory of preformation. Quite apart from all conjectures as to the detailed architecture of the id of germ plasm; it is at any rate certain that the arrangement of the determinants is quite different from that of the corresponding parts in the fully formed organism. This is proved by a study of development, and need not detain us here. Any one with a knowledge of animal embryology knows how great a difference there is between the mode of development of the parts from one another in the embryo, and their respective relation in the mature organism" (*op. cit.*, p. 65).

quired to form a single cell, is no doubt a probability. Unless we take refuge in such unmeaning phrases as formative forces, vital principles, and the like, we are obliged to assume some material unit, the basis of the phenomena of life. But we can hardly go as far as Weismann and assert that a particular kind of unit, protean though its constitution may be, his biophor, *must* exist, and is therefore no mere hypothetical affair, but a reality. To assert this is surely almost as much an error as to assert that no such units do exist. Practically when we have passed beyond the limits of vision we have entered upon the region of the unknown, possibly of the unknowable, and convenient as it may be to have a hypothesis which will enable to represent facts to ourselves in an intelligible way, we ought to be very cautious in our statement of the hypotheses. The arguments of those who plead for the existence of infinitesimal units, whether micellæ or pangenes or biophors or what not, amount to this: so far we have been able to observe with our senses, but the things which we have observed remain unintelligible to us; reason tells us that behind all this there must be something which we are at present unable to observe, and analogy leads us to believe that this something is in the form of material particles. Excellent philosophy, but is it physical science? And if the material units are conceded, is the difficulty as regards vital phenomena in any way diminished? Is it not simply moved further back? To continue with Weismann's hypothesis, the most complete and the most ably sustained of any that has been put forward: the biophors exhibit the primary vital forces, assimilation and metabolism, growth and multiplication by fission; they are also the bearers of the qualities of cells, by which is meant that each biophor has a quality of its own which it is capable of impressing on the cell of which it forms a part. As each biophor is capable of reproduction giving rise by fission to its like, it hands on the particular quality inherent in it, that is to say, it has heritable qualities, which, however, are not of much importance, since every biophor is isotropic, capable of further change by a rearrangement of its constituent molecules. Truly a protean being, this

biophor, as soon as one tries to lay hold of it in one shape it appears under another; but the point to which I wish to draw attention is not this, but the fact that the biophor is credited with all the vital capacities of the cell, and that in explaining the vital phenomena of cells by reference to biophors, the difficulties are only moved further back; the vital activities of biophors are still unexplained. The existence of ultimate vital units could be affirmed with much greater certainty if we were able to infer from their assumed structure, or their motion relative to one another, that certain consequences must follow, and to demonstrate that such consequences do follow as a matter of fact. It is the possibility of doing this which gives so high a value to the atomic theory, but we are far from being able to do it in the case of the hypothetical vital units. Weismann makes the attempt, but he is obliged to confess that "as long as we know practically nothing about the forces which act in and among biophors, it will be impossible to offer an explanation of (a mechanico-physiological) kind".¹

The evolutionary theories which have lately been put forward are not, therefore, of the nature of a general statement of fact, but are assumptions made in order to explain the causes of observed phenomena; they are dependent upon reason, not on observation, and they differ from the analogous theories of the last century chiefly in this, that the latter were founded in the first instance on an erroneous observation—that of Malpighi—whereas the former are inferences from a very large number of accurate and verified observations. There is naturally a very wide difference between the resulting theories, and the probability of the latter-day hypothesis is antecedently of a very much higher order than that of the older, although the underlying idea is the same in both cases. The argument for the new evolutionary theory may briefly be stated as follows. In the development of any multicellular organism the ovum is observed to go through a great number of typical changes in typical succession. By the sub-

¹ *Op. cit.*, p. 84.

division of the original single cell a number of cells are produced which do not remain like one another, but at fixed times in every species take up a fixed position and give rise to further cells which go through a perfectly regular set of form changes, resulting in the formation of tissues and organs in definite and determined relations to one another. These relations taken together form the character of the species. The process is one not only of cell multiplication, but also of cell differentiation, and the differentiation during the course of ontogeny must be effected in one of two different ways. Either the original cell, the ovum, divides quantitatively, so that each resulting cell is composed of similar material and only goes through its subsequent form changes as the result of its position and the reaction of the cells contiguous to it, or the ovum divides qualitatively and the resulting cells are composed of unlike material, the subsequent form changes being the result of the unlikeness of the material of which they are composed. The latter of these two alternatives is preferred, partly because in a number of instances the differentiation of the cells is apparent from the first cleavage onwards. Of the two first blastomeres, each has a distinct prospective career, each differs in its essential characters from the other. With the second, third, and fourth cleavages, further differentiation is effected, and the individual cells are stamped, as it were, with their particular characters from the very commencement. These are qualitative changes, and are not to be accounted for by the action of any external agencies; the determining force must reside within the cell, and must be the result of a different constitution effected by the separation of unlike materials which were present in the ovum. And this view is largely borne out (according to the argument) by experiments which have been made on segmenting ova; it has been shown, for instance, that if the two primary blastomeres of a frog's ovum be separated by mechanical means, each will continue to develop, not as a whole, but as a half organism, one blastomere giving rise by further subdivision to the right half, the other to the left half of the embryo. Clearly, then, the first division does not affect the mass

only, for in that case each blastomere would go through a normal development, and give rise to a complete embryo ; it must also affect the quality of the ovum, and separate off that which belongs to the right half of the future organism from that which belongs to the left half. There must be in consequence a particular architecture in the protoplasm of the ovum, an organisation of a definite kind, and of such a nature that the characters of the future organism are severally represented in the separate structural elements of the ovum, and that these become segregated in the course of cell multiplication.

It is really of no consequence to the argument whether the determining structural complexity is supposed to reside in the cell body, or in the nucleus ; it is the case that numerous considerations have led to the belief that it resides in the chromatin of the nucleus, but if it were otherwise, the main proposition would be unaffected.

The final conclusion is that, homogeneous and simple as it may appear to our vision, the ovum is an exceedingly complex and an organised body, and when this conception is joined with that of *particulæ vitales*, which go to make up the cell and to stamp it with its special characters, the further conclusion is irresistible, that there are in the germ plasm primordial form elements, of which each has an allotted course by which it proceeds to its position in the adult organism. The final result is attained when only one kind of primordial element is contained in each cell, *viz.*, that which has to determine it. Weismann extends this idea by supposing that the primordial elements are formed into groups, and that the groups, which he calls *determinants*, are segregated in the course of ontogeny until every cell, with some few exceptions, contains and is controlled by only one kind of determinant.

The essence of the evolution theory consists in the view that the primordial particles contained in the germ are of as many different kinds as there are different kinds of cells in the adult organism ; that the course followed by each is predetermined by the position which the cell or cell group which it controls will have in the adult ; and that in

the course of ontogeny the different kinds are sorted out and arranged, so that the different cells come to contain very different kinds of primordial particles, and therefore that their capacity for further change is limited in every stage by the particular kinds of particles which they contain.

This theory differs from that of the eighteenth century in substituting for a preformation of organs as such, a pre-determination of vital particles which by growth, multiplication and arrangement are to give rise to organs, or, at any rate, are to control the formative processes by means of which organs are established. But, as we have already seen, the idea of preformed organs existing as such, but in miniature, was by no means an essential part of the physiological theory of the last century. Bonnet's final conception of a germ as a "*préformation originelle dont un Tout organique peut résulter comme de son principe immédiat*" is extremely like the modern conception of germ plasm, composed of a multitude of predetermined elements.

A modern conception, derived from the theory of evolution in its larger sense, that is from phylogeny, is grafted on the theory of individual evolution, and it is held to be one of the great merits of the latter theory that it harmonises and explains the analogies of ontogenetic and phylogenetic development. This is the conception that the fixed architecture of the germ is inherited; that is to say, that it is the necessary outcome of the architecture of the preceding germ from which it was derived, just as that was the outcome of the germ which preceded it, and so on in decreasing circles of complexity to the beginning of living things. It is impossible to follow out this idea with all its consequences in the limits of an essay, but it is the essential proposition which Weismann seeks to establish in his theory of the germ plasm, and any one who wishes to understand the subject better must be referred to his work.

Bonnet and the older evolutionists were possessed of a similar idea, which is in fact a direct corollary from the theory of pre-existences or determinants. Since germs are

derived from pre-existing germs, the latter must have contained within themselves the principles of the former; hence the theory of "emboîtement," or the inclusion of germ within germ, which necessarily underwent considerable modification as germs were regarded as organised bodies in miniature, or as original preformations, immediate principles from which the whole could be developed. The views of Cuvier, adopted from Bonnet, as they are expressed in Laurillard's "Éloge," are very similar to those of to-day, and the reasoning which led to those views is parallel with the reasoning which has led to the modern theories. Cuvier believed in the pre-existence of a *radical de l'être*, a radical which existed before the series of evolutions commenced, and certainly could be traced back for several generations.

Has it occurred to those who assert that the fixed architecture of the germ determines the species, and that the species has given its impress to the fixed architecture of the germ (for this is what is meant by saying that the fixed architecture is *inherited*), has it occurred to them that this is only a restatement in another form of the old problem "whether the chick gives rise to the egg or the egg to the chick"? Trace back the successive production of germ from organism, organism from germ; try to form a mental picture of the successive grades of complexity acquired by both and transmitted from one to the other, and one is soon landed in insuperable difficulties in spite of the formal solution of Weismann. Whoever has faced this question and tried to trace back the complex transmissions of characters has arrived at the same conclusion, first expressed in a manner acceptable to biologists by Weismann, but present to the mind of Harvey, and before him to Aristotle, namely, the continuity of the germ plasm.¹

The "circuitus gallinaceus," as Harvey calls it, is

¹"Facit namque hic circuitum gallinaceum genus sempiternum; dum modo pullus, modo ovum, continuata perpetuo serie, ex individuīs caducis et pereuntibus immortalē speciem producunt" (*Exercit. de generatione*, Ex. xxviii.).

paralleled by the "circuitus theoreticus": the course of speculation seems to start from a new beginning to develop along a special course, and to become a complete organon, only to fall back again into the same germ from which it arose.

The theory of determinants, which is the modern expression of individual evolution, is not, however, universally accepted. There is another theory, which may be called epigenetic, founded on the assumption that the division of the egg is not qualitative, but quantitative. According to this view the daughter cells, at every cell division, no matter what may be their prospective character, receive exactly equal amounts as well as kinds of nuclear material, in which the elementary particles are supposed to reside. The differentiation of the resulting cells is determined in each case by cellular interaction, the development of each cell is determined by its relation to its fellows, or as it has been neatly put, "its prospective character is a function of its location". The advocates of this theory point to experiment and observation in support of it. For example, E. B. Wilson has shown that in the egg of *Amphioxus* each of the first two blastomeres, if separated mechanically from the other, goes through a normal course of development, resulting not in a half embryo, but in a complete embryo which is half the normal size. Similarly each of the first four blastomeres, if separated from its fellows, gives rise to a normal embryo of quarter size. But in the eight-cell stage the course of development becomes obscured, and definite results are not arrived at. Similar observations have been made on the eggs of *Echinus*. These experiments are held to prove that the division of the ovum must be quantitative only, since the daughter cells have the same capacity to produce the organism as the mother cell, size only excepted. In later stages, *e.g.*, the eight-cell stage, the idioplasm of each cell has become modified by the interaction of the adjoining cells, and has, therefore, lost to some degree the primitive power of giving rise to the whole organism, and this modification with the corresponding loss of formative power becomes accentuated with every

fresh cleavage, owing to the increased reaction of the more numerous constituents of the cell aggregate.¹

I am not sure that I have quite fairly represented the views of any single author. Herbert Spencer certainly considered that the physiological units, whose existence he postulated, were all alike in kind in each individual organism, and that the germ cell, from which the organism is derived, contained small groups of these units. The difference in the arrangement of units alike in kind determines the diversity of the parts of the body, according to his theory; the diversity in the constitution of the units being the cause of the distinction between different species and different individuals. On this view units are physiologically variable quantities, which act under the directing influence of the whole organism. This is very similar to Driesch's statement that the prospective character of each cell is a function of its location. Recent writers are not so explicit in the statement that all the units composing the individual are alike in kind. The position is very much altered if it is assumed, as they seem to assume, that the units composing the individual are of many different kinds, of as many kinds as there are different kinds of cells in the adult (in so far agreeing with Weismann and Roux), but that in each cell divisions all the kinds of units are transferred from mother to daughter cell. In such a case every cell would have primitively the power of going through the whole course of ontogeny, thus accounting for the phenomena of regeneration and reformation, whilst the "function of the location" would be limited to determining which of the units present should impress on the cell the character necessitated by its position in the organism. This is the view taken by

¹ "As the ontogeny advances, the idioplasm of the cells undergoes gradual and progressive *physiological* modifications (brought about by the interaction of the various parts of the embryo), without, however, losing any of its elements. The isolation of a blastomere restores it in a measure to the condition of the original ovum, and the idioplasm, therefore, tends to return to the condition of the original germ plasm, and thus to cause a repetition of the development from the beginning" (E. B. Wilson, "Amphioxus and the Mosaic Theory," *Journal of Morphology*, vol. viii., p. 609).

E. B. Wilson in the article which I have already quoted, in which he seeks to reconcile the hypotheses of Weismann and Roux with the observations made by Driesch and himself on the cleavage of isolated blastomeres. Wilson's attempts to reconcile these apparently conflicting views are attractive, since they include a reconciliation of an evolutionary with an epigenetic theory of development, as is evident from his own words: "The entire series of events is primarily determined by the organisation of the undivided ovum that forms its first term, and, as such, conditions every succeeding term. The morphological value of the individual blastomere at any particular stage is the product of two factors, one of which (the embryonic environment) is external, while the other (the nature of the idioplasm) is internal."¹

A curious confusion, as it seems to me, has been introduced into these discussions by the use of the term, "mosaic work," invented by Roux to signify "a whole formed out of several or many self-determining parts". Now there is nobody who has seen a mosaic, and knows how it was made, who would describe it as being formed out of self-determining parts. With all respect to the judgment of Roux, I have always thought of a mosaic as formed out of parts whose position was determined by forces lying altogether outside themselves, namely, by the artist who designed the mosaic, and the workmen who put the parts together, and this, I take it, would be the opinion of every sensible man. The name mosaic can only be properly applied to a whole, the parts of which owe their position to an external controlling force: it is not in the least applicable to a whole, the parts of which are self-determining. In point of fact, the name mosaic is applicable to epigenesis, not to evolution, and was so applied by Huxley long ago.² If I understand

¹ *Op. cit.*, p. 614.

² "For Schwann, the organism is a bee-hive, its actions and forces resulting from the separate but harmonious interaction of all its parts. For Wolff, it is a mosaic, every portion of which expresses only the conditions under which the formative power acted, and the tendencies by which it was guided" (The "Cell Theory," *Medico-Chirurgical Review*, xii., 1853, p. 295).

Wilson aright, his proposed modification of the so-called mosaic theory does, in some measure, justify the use of the term, since emergence of the mosaic-like character of the ontogeny from the indifferent condition of the early stages is due to the action of an external factor, *viz.*, the embryological development. This, at least, is one interpretation which might be put on his somewhat obscure reasoning. But I am not sure that he does intend to say this, but contrariwise, that the mosaic character is dependent on the internal factor, *viz.*, the nature of the idioplasm of the ovum. In this case, the use of the word mosaic is not only misleading, but mischievous.

The mosaic of Roux (and of Wilson?) determines its own pattern; the organism, according to Whitman, dominates its own development, not because of cellular interaction, that is denied, but because of some intrinsic property, an organisation which precedes cell formation and regulates it. Now the pattern of a mosaic is not determined by the forces residing within its component parts, nor is it conceivable that the organism, that is the final aggregate of parts which have been successively formed, dominates the formation of parts without which it has no existence. There is a fallacy here in the word organism. Whitman is the last who has spoken on this subject, evolution or epigenesis, and his attempts to find an explanation of vital phenomena, to discover some ultimate cause of observed sequences, are hardly more satisfactory than the attempts of those who have preceded him. He seems himself to be aware of this, for he ends by pointing out the difficulties without offering any solution. But his attempt to clear the path by breaking down the cell theory will meet with very little sympathy. He appears throughout his essay to be labouring under a grave misconception as to the nature of the cell theory as it has been accepted for many years past. He quotes the original dicta of Schleiden and Schwann, and proceeds to the easy task of demolishing them. As a matter of fact the cell theory as originally propounded by Schleiden and Schwann has undergone no inconsiderable modifications; their very con-

ception of the structure of a cell was erroneous and went far to invalidate the completeness of the doctrine which was founded on it; I refer, of course, to the supposed mode of cell formation, and the part played in it by the "cytoblastema". Some parts of the cell theory remain unshaken; it would be very difficult to deny that "the cause of nutrition and growth lies not in the organism as a whole, but in the separate elementary parts—the cells". Nor is it easy, however one may regard it, to cavil at the statement that "the whole organism subsists only by means of the reciprocal action of the single elementary parts". But that "the organism consists morphologically of cells," and that "organisation means cellular structure," are statements which nobody would for a moment give his adherence to now, nor am I aware that Schwann ever gave utterance to any such propositions. Schwann appears to have been fully aware of the complexity which must reside in cells, for he speaks of "conglomerate molecules," "a peculiar mode of union of the elementary atoms to form atoms of the second order," but, he says, he has only to deal with the question whether the cause of organic phenomena lies in the whole organism or the separate elementary parts. He is not concerned with making a hypothetical analysis of ultimate cell structure, but he did not therefore deny it. Whitman is anxious to establish a point which he calls the organism standpoint, and in order to do it he makes use of the very common method of exaggerating the erroneous views of a few individuals into a prevailing belief among biologists. Nobody who has ever considered the structure and development of the capillaries, for instance, has ever made a *fundamental* distinction between intracellular and intercellular structure; unicellular and multicellular organisms have been contrasted it is true, and the contrast is striking, but who has made a fundamental distinction between them? Are they not both known as organisms? "The organism" used as a term to express living bodies is not "fancied to carry at least two distinct organisations, the organisation of the separate cells and that of the cell united," at least not by rational biologists of my acquaintance. This may be said of

the multicellular organism but not of "the organism". The same fallacy runs throughout the whole argument; it is the *ignoratio elenchi*, the attempt to disprove what was not asserted. The existence of this fallacy makes it unnecessary to follow Whitman's argument in detail; it need only be said that by the great majority organisation, even a very considerable complexity of visible structure, is readily conceded to the single cell. To deny this would be to deny a patent fact. It follows that structure is not dependent on cell division (whoever said it was), and that "formative processes," whatever that may mean, cannot therefore be referred to cell division, but it does not follow that they are not in some measure due to cellular interaction in multicellular animals or that they are due to ultimate elements of living matter, idiosomes, which make up all living matter, are the bearers of heredity and the real builders of the organism. This is the evolution standpoint again. Whitman must have his idiosomes to explain what he found inexplicable in cells, but what explains the behaviour of idiosomes, how are they, any more than cells, the bearers of heredity and the real builders of the organism? It is a problem, he tells us, on which we must wait for more light—it is certainly wanted, for the obscurity attending idiosomes or any other biological units is very great.

Difficult as it has been to give a comprehensive account of the many theories now current, to account for the phenomena of heredity, which are seen to be associated with development, I have I think made it abundantly clear that there is a general tendency to assume the existence of ultimate structural units as necessary for the explanation of vital phenomena. The reasons for this tendency are very succinctly expressed in a sentence of Whitman's, who asserts that it is an accepted axiom that function presupposes structure. This is a statement of the morphological standpoint; let us examine it a little further. The varied functions of cells presuppose structures in cells corresponding to the functions; not molecular structures, but definite form elements, themselves of great molecular complexity—in short, an organisation. But the form elements are on all

hands admitted to exhibit vital phenomena, they themselves have functions, for that is what is meant by saying that they are bearers of heredity, that they are capable of assimilation, growth, multiplication. If function presupposes structure, the units themselves must have their structural characters to account for their functions, they must themselves be compounded of further units, and so on *ad infinitum*. The *form* standpoint, the morphological conception, involves a new doctrine of *emboîtement*. It may be answered that the molecular constitution of the form elements is sufficient to account for their functions, but, if so, why may not molecular constitution suffice for the explanation of the functions, even for the observed structure of cells? Is it really necessary to carry structural analysis beyond the point which we can recognise with our microscopes? We may concede a great complexity of molecular structure to the idioplasm of the nucleus without admitting the existence of structure or organisation in its proper sense. May we not make some use of "polarity"? The molecules in a solution may arrange themselves in definite manner and form crystals, but we do not say on this account that the molecules in the solution are arranged in definite form elements, as crystal determinants. On the contrary, the form assumed by the molecules is attributed to certain attractions and repulsions, but what the essence of those attractions or repulsions may be it passes the wit of man to conceive. At any rate it is not supposed that these inorganic forces must have bodies to dwell in, and the so-called axiom, that function presupposes form, appears to me to be nothing more than a most unphilosophical postulate, that organic forces (whatever they may be) must have bodies to dwell in.

The issue between an epigenetic and an evolutionary theory to account for the phenomena of development is narrowed down to this: Must structure and definite organisation be predicated of everything that manifests vital activity? Until very recent years the answer has been unhesitatingly no, and an epigenetic explanation of development has consequently been *conceivable*, though it has never been satisfactorily formulated. If, contrariwise, the answer

is to be yes, an epigenetic explanation is inconceivable, and an evolutionary theory is necessary. But an evolutionary theory carries with it consequences which when followed up soon land us in the inconceivable.

Whitman has concluded his article with a quotation from an essay by Huxley. I will conclude mine by another quotation from the same essay, which I humbly recommend to those who, styling themselves morphologists, are much given to philosophical speculation.

"Physiology and ontology are two sciences which cannot be kept too carefully apart; there may be such entities as causes, powers and forces, but they are the subjects of the latter, not of the former, science, in which their assumption has hitherto been a mere gaudy cloak for ignorance. For us physiology is but a branch of the humble philosophy of facts, and when it has ascertained the phenomena presented by living things and their order its powers are exhausted. If cause, power, force, mean anything but convenient names for a mode of association of facts, physiology is powerless to reach them"—a powerlessness, I may add, which is in no way diminished by the assumption of any number of ultimate bodies in which the forces may reside. I beg to submit, in conclusion, that the ascertained phenomena of development presented by living beings and their order may be expressed by epigenesis, and cannot be expressed by evolution in its narrower sense. It is possible that, when more facts are ascertained, epigenesis will have to give way, though this does not seem to me probable; but the requirements of a theory are not ascertained facts, and must not be thought to have invalidated a useful and substantial doctrine.

G. C. BOURNE.

ON OUR PRESENT KNOWLEDGE OF THE NUMERICAL VALUE OF THE MECHAN- ICAL EQUIVALENT OF HEAT.

THE subject of the mechanical equivalent of heat may be regarded as a meeting-ground for many of the explorers in the world of science. It is capable of approach by many different paths and by distinct methods, and thus affords to investigators a means of testing the accuracy of the observations by which their steps have been guided.¹ The value of this central position increases as our knowledge concerning it becomes more definite, and my object in this paper is to briefly discuss the value of the information we now possess.

Although it would be difficult to overrate the importance of an accurate determination of the numerical value of the mechanical equivalent, it would be easy to underestimate the difficulties of the achievement. Any inaccuracy in our measurements of temperature, in our values for g , or in our conclusions as to the changes in the temperature coefficient of the specific heat of water, tell with fatal effect in such an investigation.

Again, if the method of inquiry adopted is based on the work done by an electric current when passing between points at different potentials, we are in addition confronted with the possibilities of small experimental errors (whose cumulative effect may be serious) in the values of our electrical units.

It is impossible in the present article to do more than glance at the work of a few observers. Those who wish for a complete summary will find a historical table in the

¹In the discussion which followed the reading of a communication on this subject to the Royal Society in February, 1893, Lord Kelvin called attention to the fact that the discovery of the error in the B.A. ohm was due to the circumstance that the adoption of that unit as a standard of resistance caused the investigator to arrive at a value of J which was evidently outside the possible limits of that constant.

admirable paper by Professor Rowland¹ which gives the methods and results of all observers anterior to 1880, and Miculescu² supplies a further list which carries us to the year 1892. The results expressed in kilogrammetres range from 371.6 (Hirn,³ 1857) to 488.3 (Joule,⁴ 1845). The list contains many names well known and deservedly honoured in the scientific world, but unfortunately the conclusions arrived at by many of the observers are of little value.

Rowland in 1879 wrote as follows:⁵ "All the results so far obtained, except those of Joule, seem to be of the crudest description, and even when care was apparently taken in the experiment, the method seems to be defective, or the determination is made to rest upon the determination of some other constant whose value is not accurately known. Again, only one or two observers have compared their thermometers with the air thermometer, and the error thus caused may be more than one per cent. The range of temperature is also small as a general rule, and the specific heat of water is assumed constant."

With this somewhat sweeping expression of opinion I am reluctantly compelled to agree, and I would add the following to the list of errors committed by the observers: (a) Faulty determinations of the water equivalent of the calorimeter, and the assumption that its water equivalent remained constant when the temperature altered; (b) disregard of the undoubted fact that the readings of mercury thermometers vary according to their rate of rise (a circumstance which I may remark escaped the attention of Rowland himself); and (c) too great similarity in the conditions under which the experiments were performed, corroboration being sought for by a mere repetition of the experiments rather than by an alteration in the conditions,

¹ *Proceedings of the American Academy*, 1880.

² *Annales de Chimie et de Physique*, vol. xxvii., p. 206.

³ *Theorie Mechanique de la Chaleur*, 3rd edition.

⁴ *Phil. Mag.*, 3rd series, vol. xxiii.

⁵ *Proceedings of the American Academy*, 1880.

the latter of which I believe to be the only method of eliminating constant errors.

A story is related of a would-be physicist who carried his belief in the doctrine of averages to such an extent that to save himself the trouble of direct weighings he adopted the custom of asking the opinion of a large number of individuals as to the weight of a certain object—his argument being that if he obtained a sufficient number of guesses the mean result would be near enough to the truth. History does not record if he adopted the method of "least squares".

On the same principle it may be of value to give the mean of all the results referred to in the above tables. For observers who adopted direct methods, such as the agitation of water, etc., I find it to be 431.1 kilom. per thermal unit C.; for those who adopted what may be termed indirect methods, such as the velocity of the propagation of sound, etc., 421.0.

Undue attention has been devoted by many observers to the methods adopted for the conversion of mechanical work into heat as compared with the regard paid to that vital point—the thermometry. Some have even considered it sufficient to employ the ordinary mercury scale of temperature, and the unfortunate part of such want of attention is, that it is almost impossible, even with the light of later investigations, to estimate the consequent errors. The thermometers have in most cases disappeared, and, when still available, the conditions under which they were used are so uncertain that a comparison with our present standards is of little avail. The reading of some of the papers above referred to is to me a painful experience. The devices employed for converting nearly the whole of the energy into heat, the expedients for estimating the residual amount of energy converted into other forms, are such as to compel the admiration of the reader, but, although so much ingenuity has been directed to the adornment of the upper stories, the foundation—the measurement of temperature—has been neglected, thus rendering the whole edifice unstable.

I select from the whole list the results obtained by Joule, 1843-78, Rowland, 1879, Miculescu, 1892, and I would venture to add my own of 1888-93, as those to which attention should chiefly be directed, because these authors have (especially in the case of Rowland) given the data for their thermometry. True, that Joule appears to have paid little attention (comparatively speaking) to this matter, but, as will be shown later, we are to some extent able to repair this omission.

Rowland devoted a great portion of his paper to the description of the comparisons of his mercury and air thermometers. On page 498 of my own paper I have, however, given my reasons for the following statement: "A study of Rowland's tables xi. to xv. leads to the conclusion that the discrepancy between individual observations, due to the above-mentioned causes, in some cases amounted to as much as 0.3° to 0.64° C. . . . and appears to justify the conclusion that the value of Rowland's temperature range 14° to 25° C. may be in error by as much as 0.020° C.," that is, over the above range, an error of 1 in 550.

Fortunately, the thermometers used by Joule are still in existence, and the magnitude of the errors arising from imperfections in his thermometric standards has been approximately ascertained; for Joule himself in 1879 made a careful comparison of his thermometer with one which had been standardised by Rowland, the outcome being to raise Joule's final results from 772.55 to 776.75 ft. lbs. (F.) in latitude of Greenwich, whereas if we apply the thermometric correction to *all* his published, instead of his final, results the corrected mean becomes 779.15.

Even in this case, however, we have not sufficient data to apply the correction with accuracy, for no record has been found, beyond the published numbers, of the conditions under which the comparison between the thermometers was made, although I understand from Professor Schuster (in whose possession the Joule thermometers now are) that search has been made for such records. Again, it must be remembered that the application of the above

correction detracts greatly from the *independent* authority of the determinations by these two physicists. If it could be shown that an error existed in the thermometry of Rowland, the resulting correction would have to be applied not only to his values but to those of Joule. The methods employed by Rowland were otherwise so perfect that if sufficient evidence could be produced to finally establish his temperature measurements I, for one, should be inclined to accept without reserve his conclusions as to the value of the mechanical equivalent.

Happily there is a good prospect of more light on this point. Professor Schuster has for some time been engaged in a separate determination of the mechanical equivalent, and I anticipate with much interest the publication of his results. At the same time he is (I believe) re-standardising the Joule thermometers, and in my opinion the importance of this portion of his investigation may prove as great as the achievement of a revaluation of J. If, as I trust may be the case, he is led to the conclusion that the temperature range given by the previous standardisation is faulty, we shall have the means of applying to the results of Rowland and Joule an approximate correction which may bring them into greater harmony with the latest investigation.¹ I indicate later my reasons for believing that the discrepancy between the results obtained by Rowland and myself has its origin in thermometric errors. I have applied to my own thermometry every test which appears to me to be possible; it remains to be seen whether Rowland's temperature range is capable of such a scrutiny, and I am glad to think that this important investigation is in the able hands of Professor Schuster.

With regard to the temperature work of M. Miculescu he adopted a thermo-electric couple of platinum and iron,

¹ No doubt changes have taken place in the Joule thermometers with lapse of time. Although such time changes may have caused considerable alteration in the position of the zero points, it is improbable that they will affect determinations of *differences* of temperature when made by the same thermometer.

whose indications he compared with a mercury thermometer previously standardised by the Bureau International des Poids et Mesures. Admirable as were his arrangements I consider that the comparison of electro-motive forces is better adapted for the *detection*, than for the accurate *measurement* of small differences of temperature.

This is hardly the place in which to enter into a discussion of the question, and I only here give my opinion for what it is worth, though I have reason to believe that it is shared by others.

Again, he gives no precise details in his published paper of the circumstances under which the readings of the mercury thermometer were taken—such as the constancy of the temperature, the rate of rise (if any), the observed changes of zero, etc., nor does he give any record of the results of the differences between repeated comparisons at the same temperature; thus it is impossible to estimate his probable limit of error.

There is little doubt that measurements of resistance can, under favourable circumstances, be made with greater accuracy than comparisons of the electro-motive force due to a thermo-electric couple.

The investigations by Professor Callendar and myself have, I think, placed beyond question the relation between the platinum and the air thermometer over a range of 0° to 600° ¹ C., and the almost exact correspondence subsequently discovered (a difference of 0.005° C. in elevation, and of 0.001° in range between 14° and 25° C.)² between the mercury thermometers used in my investigation (which were standardised by means of platinum thermometers) and the

¹Callendar, *Phil. Trans.*, A, 1887.

„ *Phil. Mag.*, July, 1891, and January, 1892.

„ *Journal Iron and Steel Institute*, No. 1, 1892.

Callendar and Griffiths, *Phil. Trans.*, A, 1891.

Griffiths, Brit. Assoc. Report, 1890.

„ *Phil. Trans.*, A, 1891.

„ „ „ „ 1893, pp. 420-433.

„ *Phil. Mag.*, 1891.

² *Phil. Trans.*, 1893, p. 430.

nitrogen thermometer of the Bureau International appears to place the measurements, over this range at all events, on a sure foundation.

Since the publication of my paper in the *Transactions*, Professor Callendar and I have conducted a laborious series of comparisons between the mercury thermometer and a new and beautiful form of the air thermometer invented by himself. Its indications are independent of changes in atmospheric pressure during the experiments; thus no observation of the length of a mercury column is necessary, and one great cause of experimental error is avoided.

The results have now been published,¹ and although in some respects unsatisfactory, they are sufficient to clearly establish a limit of range-error, not exceeding 0.03° C. of the nitrogen thermometer over a range of 14° to 25° C. I therefore venture on the statement that the evidence is in favour of the greater accuracy of my temperature measurements when compared with those of the observers I have mentioned.

Another great difficulty faces the experimenter, *viz.*, uncertainty as to the thermal unit.

The condition of the science of calorimetry will continue unsatisfactory until some definite conclusion is arrived at as to the fundamental unit. The old definition—the amount of heat required to raise unit mass of water from 0° to 1° C.—dies hard in spite of its absurdity, and it is time that a successor was appointed. I have suggested the following definition, “The quantity of heat required to raise unit mass of water through 1° C. of the air thermometer at 15° C.,” and I trust that this may be adopted.² Until this matter is settled it is impossible to satisfactorily compare the values of J obtained by different observers, for we

¹ *Proceedings Royal Soc.*, January, 1894.

² I am glad to see that Mr. Glazebrook in the excellent text-book on Heat, which he has just brought out, adopts a rational range of temperature, *viz.*, 4° to 5° C. I still, however, maintain my preference for the range I have suggested.

must either assume the value of a temperature coefficient of the specific heat of water obtained by one observer before we can express the results of other experimenters in terms of the same unit, or we must give the different results in terms of different units according to the mean temperature of the range over which the observations were conducted, in which case it becomes almost impossible to estimate how close is the agreement. This difficulty is a very serious one, and to me it appears to be useless to further increase the accuracy of the methods employed for determining the value of J until this fundamental inquiry is completed. The observations of Rowland indicate a minimum value for the capacity for heat of water about 33° C. My own observations have not extended beyond 26° C., so I have deduced from his tables (for the purposes of comparison) the expression for the capacity for heat of water over the range 14° to 26° C. which can be approximately represented in the form—

$$1 \cdot 000400 (\theta - 15).$$

My own result over the same range gives—

$$1 \cdot 000266 (\theta - 15).$$

I regret that I have been unable to procure the full work of Professors Bartoli and Stracciati on this subject, and I have only this week succeeded in obtaining any information beyond that conveyed by a note in *Nature*, July 27, 1893. A copy of the *Journal de Physique* for December, 1893, has, however, just come to hand, and it contains a full table of their experimental results together with a short description of the methods employed. This summary does not give the numbers resulting from the repetition of experiments under similar conditions, and it is therefore difficult to estimate the probable limit of experimental errors.

The table contains eleven columns, of which II. to VII. give the specific heat of water for every degree from 0° to 31° C. deduced from the results obtained by the immersion in water of balls of different metals at the temperature of steam, the mean result of these experiments being given in Col. VIII. The numbers in Col. IX. were

obtained by the addition of water to water, while X. gives the mean of the different methods, and XI. gives the values as deduced from the formula—

$$C_t = 1.006630 - 0.000593962t \\ + 0.000004338650t^2 + 0.000000425520t^3 \\ - 0.000000002819t^4,$$

the unit being (I am glad to see) the capacity for heat of water at 15° C.

I quote the numbers given in Cols. VIII., IX., XI. for each five degrees of temperature only.

Temp.	Col. VIII.	Col. IX.	Col. XI.
0	1.00551	1.00777	1.006630
5	1.00333	1.00434	1.003820
10	1.00140	1.00157	1.001522
20	.99946	.99949	.999439
25	1.00025	.99986	1.000040
30	1.00264	1.00111	1.001921
35			1.001570

(No direct observations appear to have been taken above 31°, and therefore the value at 35° is interpolated.)

It does not appear to me that the numbers given in Cols. VIII. and IX. (which sum up the whole of the experimental evidence at the temperatures quoted) justify the use of such a formula as that given above; at all events experimental results such as those at temperatures 0°, 5°, 25°, and 30° seem scarcely capable of a strain¹ which is too great for any physical measurements that I am acquainted with.

The experimental results are of great value, the more especially as it is evident that the observers devoted much time and attention to the standardisation of their thermometers.

The experiments themselves agree with the formula in giving a minimum value at about 20° C., and on this point, therefore, the authors differ widely from both Rowland and myself.

¹ For example, Col. VIII. gives $1 + .000025 (\theta - 15)$ as the capacity for heat over the range 15° to 25° C., while Col. IX. gives $1 - .000014 (\theta - 15)$ over the same range.

It is evident that this matter requires further investigation, for the discrepancies are serious.

I think, however, there is no doubt as to one conclusion, *viz.*, that the capacity for heat of water diminishes as its temperature rises, provided the temperature be less than 20° C.

Dr. Guillaume suggests that the temperature at which the specific heat of water is a minimum should be selected as the standard, but this point is not yet sufficiently established for the proposal to be carried into effect.¹

Whatever method be adopted for the determination of *J*, the numerical results depend upon the value of *g*. Any error thus introduced is, however, of little consequence, since every observer naturally records the value assumed for his own locality, and thus if any error be subsequently discovered the resulting correction is easily applied.

If the method adopted be an electrical one the inquirer is dependent on two of the following three constants :—

- (1) The electro-motive force of some standard cell.
- (2) The electro-chemical equivalent of some element.
- (3) The value of the ohm.

The traveller by this route is therefore less independent than the inquirer who adopts a more direct path.

When, with the assistance of Mr. G. M. Clark, I embarked on this investigation, our desire was not so much to determine the actual value of *J* as to test the validity of the determinations of the electrical units and to trace the changes in the specific heat of water. I confess that I entertained a hope that our results might be in agreement with Rowland's, and if this had been the case the existing system of electrical measurements might have been regarded as firmly established. As it is, the approximation is sufficient to prove that any residual errors are small. The want of harmony is, however,

¹I am glad to hear that Dr. Chappuis has embarked on this investigation.

clearly due to the thermometry rather than to experimental errors in the electrical standards. I extract the following from my paper in the *Transactions*: "No change in the value of the various units, or constants, involved in this investigation could bring our results into absolute agreement with those obtained by Rowland, since, owing to the difference in the expressions for the temperature coefficients of the specific heat of water, it is inevitable that our conclusions should agree at some one temperature; but must necessarily differ when expressed in terms of a thermal unit at any other temperature, and thus changes in the values of the units would only alter the temperature of agreement. For example, Dr. Guillaume has pointed out to me that the experiments of Commandant Defforges lead to the conclusion that the value of g at Greenwich should be increased from 981.17 centims. to 981.24 centims. A similar correction would slightly increase Rowland's value of J , and thus cause our point of agreement to be about 12° C. instead of 11.5° C. Again, the value of g , assumed by Lord Rayleigh (*Phil. Trans.*, A, 1884, p. 427), would have to be slightly increased, and the resulting values of the electro-chemical equivalent of silver, and of the absolute electro-motive force of a Clark cell, would require modification, but the only result of any such change would, as before, be to shift the temperature of agreement.

"It is, therefore, evident that the difference is chiefly due to errors in thermometry."

This method of testing our electrical units could only be satisfactory if a direct determination of the equivalent by mechanical work was accomplished with the same thermometers used under the same conditions as in my late investigation; harmony between the results would then be a clear indication of the validity of our system of electrical units, for the errors arising from faulty thermometry would be of small importance and the continuation of the experiments over the same range would avoid discrepancies which have their origin in erroneous conclusions as to the capacity for heat of water.

I have reason to hope that such an investigation is about to be undertaken in Cambridge, and it will, I trust, lead us on to firmer ground.

A few remarks on one other point. I have already indicated the importance of changes in the conditions under which the experiments are performed.

Rowland's determinations are, I consider, deficient in this respect. It is difficult to ascertain, from his tables, to what extent he varied the mass of the water and the rate of the work done. He appears to have changed his mass of water from about 5 to 8 kilos., and the work per kilo. seems to have varied but slightly.

The method adopted by Miculescu enabled him to employ large masses of water—his variation ranging from 5 to 18 kilos. Small errors are of much less importance when weights such as these are used, especially when the method employed, as in the case of Rowland, involves estimation of the water equivalent, losses by radiation, etc. In this respect, their conditions are distinctly superior to mine. This applies more particularly to the work of Miculescu, for the method he adopted reduced errors of the above description to a minimum. In my paper I have given my reasons as to why we were compelled to work with comparatively small masses and how the resulting evils were counterbalanced by other advantages.

During our experiments we were, however, able to vary the conditions to an extent not attempted by either Rowland or Miculescu. The rate of production of heat was continually altered (the maximum rate as compared with the minimum was as nine to one) and the mass of water was in some experiments nearly three times as great as in others. The close agreement between results obtained under such varied conditions greatly strengthens the conclusions arrived at.

The following table gives a summary of the results obtained by the observers I have referred to, expressed in kilogrammetres in latitude of Greenwich ($g=981.17$).¹

¹My values as given in this table differ slightly from those published in the *Transactions*. The reasons for the alterations are given in

TABLE II.

	J.	In terms of a thermal unit at
Joule's later experiment - - - 1878	426.26	14.6° C.
Mean of all Joule's published results - - - - 1843-78	427.60	14.5° C.
Rowland - - - - - 1880	427.04	14.6° C.
Miculescu - - - - - 1892	426.60	10 to 13° C.
Griffiths - - - - - 1893	427.76	15° C.

As previously pointed out Joule's results are here given as corrected after the comparison with Rowland's thermometer, hence they have but little independent authority.

Again, the mean temperature of Joule's temperature ranges is difficult to estimate rightly, and 14.6° C. can only be regarded as an approximation.

For purposes of reference and comparison it may be convenient if I give a table of these values expressed in terms of the different units usually employed. In each case $g=981.17$ or its equivalent in feet, the thermal unit is that at 15° C. or 59° F., and the value at this temperature is obtained by assuming the truth of my temperature coefficient of the specific heat of water. The correction thus introduced, however, is here very small, as will be seen on comparing Col. I. in Table III. with Table II.

Proc. Royal Soc., January, 1894, and they are due to the discovery of an error in arithmetic. I have here made a further small correction, amounting to 1 in 4000 only, which I did not feel at liberty to make in the above communications, where I felt bound to adhere rigidly to the actual numbers obtained by experiment. As I mentioned in the record of the observations (p. 386), there was reason to believe that, although the Clark cells used by me were for several days in the same bath as the Cavendish standard, the temperature of the standard was slightly higher, owing to its containing vessel projecting above the water. As it was impossible to accurately ascertain the actual temperature within the standard (no thermometer having been included in the cell) we did not attempt to make any correction. On reflection, I feel convinced that it is more probable that the cells differed in temperature by $\frac{1}{4}$ ° C. than that they differed in E.M.F. As I am here estimating probabilities I have assumed that this difference in temperature existed.

TABLE III.

	Kilogr. and C. I.	Ft. lbs. and C. II.	Ft. lbs. and F. III.	Ergs and C. IV.
Joule's (later experiments)	426.2	1398.2	776.8	4.182×10^7
" (all published results) - -	427.6	1402.5	779.2	4.195×10^7
Rowland - - -	427.0	1402.1	778.9	4.190×10^7
Miculescu - - -	426.2	1398.1	776.7	4.182×10^7
Griffiths - - -	427.8	1403.2	779.6	4.197×10^7

I do not see that any advantage is gained by taking the mean of these values; we must weigh the evidence in each case, and use our individual judgment; mere counting of heads will not suffice.

The result of Professor Schuster's investigations may lead to a modification of the values of Joule and Rowland as well as add another determination of great weight to the list.

I would suggest that, in the meantime, the traditional 1390 and 772.55 should disappear from our text-books and be replaced by (say) 1402 and 779.

E. H. GRIFFITHS.

RESEARCHES ON PROTEID METABOLISM,
BY E. PFLÜGER.

IT is generally accepted at the present day, in consequence chiefly of Voit's researches and writings, that :—

First, the energy for muscular work is afforded by the consumption, not of proteids, but of carbohydrates and fats.

Secondly, the fat in the body is formed from all three classes of food-stuffs, proteids, carbohydrates and fats, taken in with the diet.

Thirdly, the proteid of the food has a twofold destiny, a small part going to repair tissue-waste, and being stored up as tissue or morphotic proteid, while the larger part enters only into the circulating juices of the body as circulating proteid, and is broken up within twenty-four hours after its entry into the body, to give rise to a corresponding amount of urea.

The work by Pflüger and his pupils, which is presented to us in the appended papers, is directed to show that all of these three statements are incorrect. We may consider, in the first place, the question of the *source of muscular energy*. It was strongly maintained by Liebig that all the muscular work of the body was done at the expense of the proteids, the fats and carbohydrates, by their oxidation and disintegration, merely serving for the production of heat. Experiments however, carried out by Fick and Wislicenus, Voit and others, showed that muscular exercise gave rise to no increase in the amount of urea excreted, or that in some cases where a trifling increase was produced, the increase, or, indeed, the total amount of urea excreted, was insufficient to account for the energy expended on doing the work. On the other hand, it was found that muscular work gave rise to a great increase in the excretion of CO_2 and in the amount of oxygen absorbed, so that some carbonaceous material, probably sugar, was looked upon as the chief source of muscular energy.

Argutinsky (1), who has re-examined this question, finds

that muscular work does give rise to a definite increase in the excretion of urea. This increase, however, is observed, not on the day on which the work is performed, but on the two succeeding days. He calculates that the increased oxidation of proteid, evidenced by the extra secretion of urea, will account for the energy expended on the days on which work was done. The work consisted in climbing, on four separate occasions, to a height of 1000 to 1300 metres, and the expeditions lasted from five to eight hours.

In (2), Pflüger, on the ground of experiments performed on dogs, re-affirms Liebig's dictum, *i.e.*, that proteid is the chief, if not the only source of muscular energy. He employed a lean dog, weighing about 30 kilos., which he fed on nearly pure proteid diet (lean meat). The amount of fat and carbohydrate contained in the meat was not sufficient even for the work of the heart. On this diet he found that the dog could work perfectly well, and was in an excellent state of health at the end of some months, showing that, in this case, the energy for the production of muscular work (drawing a cart) must have been afforded by the combustion of proteids. In the experiments, periods of rest alternated with periods of severe work. The amount of meat required to maintain the dog's weight constant and nitrogenous equilibrium was first ascertained for a period of rest. If the dog was then made to do a certain amount of work on the same diet, the output of nitrogen *excreted* became larger than the income, and the dog lost weight. In order to maintain a condition of equilibrium, it was necessary to increase the amount of meat, and the increased food required was proportional to the amount of work done. Thus when the dog performed 109,608 kilogrammetres, he required 496.5 grms. meat more than during a resting period. This meat contained 15.98 grms. N. From this he concludes (allowing for the small amount of fat in the meat) :—

1 gram. N. = 6409 kilogrammetres.

According to Rubner :—

1 gram. N. in meat in combustion = 14,909 kilogrammetres.

So that 42.9 per cent. of the energy of the food has appeared as work. But meat only contains about 80 per cent. proteid, so that 1 grm. N. in proteid enables the doing of 7456 kilogrammetres. Hence 48.7 per cent. of the energy of proteid taken in as food appears as work—an enormous efficiency.

As we should expect, this dog required a greater quantity of food when the external temperature was lower, and the amount of heat that had to be produced in the body greater. The experiments described above were made when the external temperature was $+9.5^{\circ}\text{C}$. A month later, when the temperature was -8.9°C ., the dog required a larger quantity of meat, in the proportion of 4 to 3.

When work is done without increasing the food-supply, the body-weight diminishes rapidly at first, and then more and more slowly, until nitrogenous equilibrium is once more established. Under the same conditions, the nitrogenous excretion is increased at first, but not nearly to the same extent as when the animal gets sufficient food. The increase in the proteid disintegration now only accounts for $\frac{1}{4}$ to $\frac{1}{2}$ of that necessary for the production of the energy expended on doing work. There must hence be a sparing of the expenditure of energy in the other vital processes, so that proteid, which before was used up in some other organs of the body, is now expended in the muscles. In the disintegration of the proteid produced by muscular work, the CO_2 is at once eliminated, while the corresponding amount of nitrogen does not appear until the next day, and the increased excretion of urea lasts two or three days (cp. Argutinsky).

According to Pflüger, the generally accepted theory that, with a sufficient administration of fat and carbohydrates, muscular work causes no increased nitrogenous metabolism, is wrong. Even when the animal is putting on fat, increased work causes some increase in nitrogenous metabolism.

Pflüger's final conclusion in this paper is of considerable importance. He shows that the metabolic requirements of an animal are conditioned solely by the weight of proteids

("Fleischgewicht") it contains. The non-nitrogenous constituents of the body, such as glycogen and fat, are dead material, and do not affect the metabolic requirements. Only the proteids of the body are living. Hence a fat animal has apparently a small nitrogenous metabolism, in comparison to its weight, so much of this being due to dead ballast.

This view of the predominant importance of proteids for the performance of muscular work is consonant with the ideas on the subject which we in England have acquired from our experience in training men and animals to be the best muscular machines possible. The essence of training consists in increasing the quantity of proteids in the food, diminishing the carbohydrates and fats, and exercising all the muscles as much as possible. But in spite of Pflüger's arguments, we have no definite facts to exclude the possibility of sugar being the immediate source of muscular energy. We know for a certainty that sugar and glycogen may be formed from proteid, and this formation may go on in Pflüger's dog which is fed with a purely proteid diet. An increase in the amount of work done would necessitate the production of a greater quantity of sugar, and since this can only come from proteid, there must be a greater disintegration of proteid and an increased excretion of urea, so that this increased excretion would be merely a secondary result of the doing of work. It is still quite possible that, as Bunge concludes, muscular work may be performed at the expense of any of the three classes of food-stuffs. The strongest argument in favour of Liebig and Pflüger's views is still, not their carefully carried out experiments, but our common experience that a man would run a mile better on beefsteaks than on pounds of grape sugar.

ON THE FORMATION OF FAT IN THE BODY.

It is generally considered that fat may be formed from all three classes of food-stuffs, and Voit looked upon proteid as the chief, if not the only source, of fat, the fats and carbohydrates of the food only increasing the fat of the body by their sparing influence on the proteids of the food. The

chief argument for the formation of fat from proteid is afforded by some experiments of Pettenkofer and Voit, in which the nitrogenous income and output of the animal were measured, as well as the evolution of CO_2 . In many cases in which the animal was fed on lean meat, it was found that all the nitrogen taken in with the food appeared in the urine, but there was a deficiency in the carbon; so that part of the carbon had been stored up in the body, presumably as fat. In (3), Pflüger criticises these experiments in detail and shows that Pettenkofer and Voit's conclusions were founded on faulty assumptions, and that in these experiments there was really a consumption and not a deposition of fat.

In the first place, Voit did not take into account the fat and carbohydrate contained in the meat used, which in their experiments were equivalent to 10·8 grms. fat a day. Moreover, in reckoning out the daily balance sheet of the animal, they made use of an erroneous analysis of the meat. Voit did not analyse every separate sample of meat given to the dogs, but assumed its composition from previous analyses of meat. Voit, in previous analyses, found that meat contained 3·59 per cent. N. For his balance sheets, however, he arbitrarily adopts the figure 3·4 per cent. N. According to Voit, therefore, the proportion of nitrogen to carbon in the meat used was $\frac{1}{3\cdot684}$. According to analyses by Rubner, carried out in the Munich laboratory, it is $\frac{1}{3\cdot28}$, but this does not take into account 0·5 per cent. glycogen contained in the meat, so that the real proportion, according to Pflüger, would be $\frac{1}{3\cdot22}$. Making this alteration in the assumed composition of the meat given, Pflüger recalculates all Pettenkofer and Voit's experiments, and finds that in all of them the amount of carbon excreted exceeded the amount taken in with the food, so that the animal was really consuming the fat of its own body. In no case, according to Pflüger, can fat be produced in the body from the proteid of the food. As the proteid of the food is increased, so the nitrogenous metabolism rises. If any of the proteid is retained in the body, it is retained as proteid and not as fat.

After disposing of Voit's experiments, Pflüger considers certain other arguments which have been adduced in favour of the formation of fat from proteid.

A. Bitches, during lactation, have been found to give a milk richer in fat on a proteid diet than on a diet of fat. Pflüger points out that in this case it has not been proved that the extra fat appearing in the milk has not been derived from a transportation and change of the fat already deposited in other parts of the body.

B. Radziejewsky is quoted by Voit as showing that fat taken in with the food is not directly deposited as such in the body. Pflüger points out that Radziejewsky's experiments prove the exact opposite. Moreover the direct deposition of fat has been shown by many subsequent observers (Munk, Lebedeff).

C. In fatty degeneration and phosphorus poisoning, the fat is universally assumed to come from the disintegration of the proteids of the cell. Pflüger points out that the absolute amount of fat formed under these circumstances is very small and may come from the transformation of carbohydrates already existing in the body.

D. In the ripening of cheese there is a formation of fat from proteid, but in this case the change is effected by fungi and not by animal organisms. It is possible too that, in Hofmann's experiments on the production of fat by fly-maggots on putrid blood, the fat was first formed by the organisms of putrefaction and was merely eaten up by the fly-maggots and deposited in their tissues. It has not been shown that fly-maggots can convert the proteid of the blood into fat in the absence of these low vegetable organisms.

Pflüger's own method of experiment and his results are given at length in (4). In these he used dogs which were trained to pass their urine when required. He points out that only with such animals is it possible to obtain any correct information of the nitrogenous metabolism. He criticises severely the researches in which the urine was collected by putting the dog in a cage with an inclined bottom, since both urine and fæces adhere to the hairs of the animal as he rolls over, and one can never be certain

that the urine passed on one day really represents that day's nitrogenous excretion. The meat used for feeding the dogs was the leanest that could be procured. A slaughterer at Cologne had orders to telegraph to the professor at Bonn whenever a particularly scraggy beast was to be killed, and a servant was at once sent to get a sample of the meat. The amount of fat in this sample was determined, and, if the percentage was low enough, several hundred pounds of the meat were purchased. This meat was finely minced in a sausage-machine, so as to ensure uniform composition, and then was packed in tin boxes, sealed and sterilised. A sample of this meat was accurately analysed, so that the exact composition of the food used in the experiments was known, and the relation of nitrogen to carbon had not to be guessed at, as in Voit's experiments. I may here summarise Pflüger's conclusions.

1. A dog can live a perfectly normal life on a diet of which the combustible constituents are nearly pure proteid.

2. The smallest possible amount of proteid that must be given to an animal to maintain its weight constant when no fat or carbohydrate is given at the same time (Nahrungsbedürfniss) = 2.07 grms. N. per kilo. body-weight.

3. The amount of food-proteid necessary is conditioned solely by the amount of flesh on the animal, and is not influenced by the fat or carbohydrate contained in the animal.

4. The disintegration of proteid increases *pari passu* with the amount given in the food, a small quantity of the excess being stored and adding to the weight of the animal. The animal, however, cannot digest more than 30 to 40 per cent. in excess of the necessary amount of proteid. Therefore, to fatten an animal, one must call into play all the digestive mechanisms, *i.e.*, use a mixed diet containing fats and carbohydrates as well.

5. If an animal receives an amount of proteid not exceeding the necessary amount, increased administration of fat or carbohydrate does not increase the metabolism, but the whole excess is stored up as fat. As proteid has no immediate influence on fat-formation, a fattening diet

should contain as much of the cheap carbohydrates and as little of the dear proteid as possible.

6. The non-nitrogenous food-stuffs are only oxidised when the amount of proteid given at the same time is insufficient for the animal's total requirements.

7. To increase the amount of meat on an animal, the proteid given in the food must exceed the indispensable minimum.

CIRCULATING PROTEID.

If an animal be starved, the daily excretion of urea sinks rapidly for the first few days, and then for a considerable time remains very nearly constant. It might be thought that if, during this time, an amount of proteid were given to the animal, containing a proportion of nitrogen equivalent to that which the starving animal was excreting, the loss of nitrogen to the body would be checked, the loss of nitrogen in the urine being replaced in the tissues by the nitrogen of the food. This is, however, not the case. After the administration of proteid to the starving animal, the quantity of urea excreted is almost doubled, showing that nearly the whole of the proteid taken in is disintegrated within twenty-four hours, and excreted with the urine. In order to produce a condition of nitrogenous equilibrium, it is necessary to give the animal two and a half times the amount of proteid corresponding to the nitrogen that is excreted during starvation. Voit has explained this fact by supposing that the proteid taken in with the food has a twofold destination in the body, part of it going to supply the tissue-waste, and being built up into the living protoplasm of the tissues ('morphotic' or 'tissue proteid'), while the other and greater moiety ('circulating proteid') passes into the juices that bathe the protoplasmic elements of the cells, and is rapidly broken up and oxidised there, without at any time forming an integral part of the protoplasm.

This teaching of Voit has been subjected to searching criticism by Pflüger (6). He shows, in the first place, that

Voit himself has never clearly indicated what is meant by circulating proteid. Originally, at any rate, Voit looked upon both blood-plasma and lymph as circulating proteid. In his later writings, however, Voit speaks of the blood as an organ, and confines the conception of circulating proteid to the proteids of the tissue-juices, that is to say, of the lymph. According to this theory, the greater part of the processes of oxidation and disintegration must take place outside the cells, whereas the work of Pflüger and his pupils has shown that the seat of oxidation is the living cell, and that little or no metabolic changes take place within the blood or lymph. According to Voit, the greater excretion of urea in a proteid-fed animal is due to the fact that there is an increased circulation of a fluid that is rich in proteids round the cells. According to Pflüger's view, however, the presence of a greater or less amount of proteid in the nourishing medium would not be the determining factor for the amount of urea formed, which would be regulated simply and solely by the condition of the cells themselves. At his suggestion Schöndorff has undertaken an experimental investigation of the question (7). Departing from Schröder and Minkowsky's experiments on the seat of formation of urea, Schöndorff led defibrinated blood alternately through the hind limbs and the liver of another dog. He hoped in this way to get the products of metabolism of the tissue of the limbs, and then to convert these into urea by passing the blood through the liver.

In one set of experiments the blood from a dog that had been starved for five days was led through the organs of a well-fed dog. In these experiments he found that, without exception, the urea in the blood was largely increased at the end of the experiment.

In a second series of experiments the blood of a fasting animal was led through the hind limbs and liver of a fasting animal. In these the amount of urea in the blood was unaltered.

In a third set, blood of a well-fed animal was led through organs and liver of a fasting animal. In these cases the amount of urea was always diminished.

From these experiments Schöndorff draws the following conclusions :—

1. The extent of proteid metabolism depends on the nutritive condition of the cell and not on the amount of proteid contained in the circulating tissue-juices.

2. The amount of urea contained in the blood varies with the condition of the animal. The blood of a fasting dog contained 0.0348 per cent. urea as a minimum. The maximum amount of urea in the blood of a fed dog was 0.1529 per cent.

3. Urea is manufactured in the liver out of nitrogenous substances which have been produced in the other organs. These substances are probably salts of ammonia.

Pflüger then would explain the course of events in starvation as follows : An animal cell desires above all things proteid food, and when it can get enough of this feeds upon nothing else. Only when proteid is lacking will it take up fat or carbohydrate. Thus, while a dog is fed on a rich mixed diet, he lives practically on proteid alone, storing up the fats and carbohydrates of the food as fat. If food be now withdrawn, the animal must live either at the expense of his own living tissues (proteids), or must attack the stored-up fats in his body. The latter, as a matter of fact, takes place. The animal now spares the precious proteid and lives on the fat of his own body. Hence comes the great fall in the excretion of urea that is observed in starvation, the consumption of proteid sinking to the indispensable minimum. If now a proteid meal be given, the cells of the body return to their former way of living, and satisfy as much of their needs as possible at the expense of proteid, so that the urea excretion rises almost in proportion to the food given. In order to attain nitrogenous equilibrium, it is necessary to give the cells enough proteid for their total requirements, *i.e.*, two or three times as much as would correspond to the nitrogenous excretion during hunger.

These views of Pflüger have the double advantage of being simple and at the same time in accord with the observed facts of experiment, and will no doubt displace the hazy and indefinite conception which has given birth to

the dissociation of the metabolism of the cell from the metabolism of the tissue-juices.

Note.—The method employed by Schöndorff for determining the urea in the blood was as follows: One volume blood is treated with two volumes of a solution of phospho-tungstic acid in dilute hydrochloric acid, allowed to stand twenty-four hours and filtered (Filtrate I.). By this means the proteids and nitrogenous extractives (excluding urea) are precipitated. Filtrate I. is rubbed in a mortar with calcium hydrate to an alkaline reaction and filtered (Filtrate II.). Filtrate II. is divided, one part being used to determine ammonia by a modification of Schlösing's method. In another part of Filtrate II. the total nitrogen is estimated in the following way: 10 grms. of crystallised phosphoric acid are weighed out into a long-necked flask of one litre capacity. A measured quantity (15 or 30 c.cm.) of Filtrate II. is then added, and the mixture heated three hours in a drying oven to 230°-260° C. The brownish syrupy residue at the bottom of the flask is then dissolved in boiling water, 70 c.cm. caustic soda (sp. gr. 1.25) and talc added to the mixture, which is then heated. The ammonia which comes off is collected in a measured amount of titrated H_2SO_4 . From the nitrogen found in this way, the nitrogen present as pre-formed ammonia is subtracted. The remainder represents the nitrogen present in the blood in the form of urea.

- (1) Argutinsky. Muskelarbeit und Stickstoffumsatz. Pflüger's *Archiv*, xlv., p. 652.
- (2) Die Quelle der Muskelkraft. *Ibid.*, l., p. 98.
- (3) Ueber die Entstehung von Fett aus Eiweiss im Körper. *Ibid.*, li., p. 229.
- (4) Ueber Fleisch-und Fettmästung. *Ibid.*, lii., p. 1.
- (5) Die Ernährung mit Kohlehydraten und Fleisch oder auch mit Kohlehydraten allein in 27 von Pettenkofer und Voit ausgeführten Versuchen. *Ibid.*, lii., p. 239.
- (6) Ueber einige Gesetze des Eiweissstoffwechsels. *Ibid.*, liv., p. 333.
- (7) Schöndorff. In welcher Weise beeinflusst die Eiweissnahrung den Eiweissstoffwechsel der thierischen Zelle? *Ibid.*, liv., p. 420.
- (8) Jacobsthal. Versuche über die Fettbildung bei der Reifung des Käses. *Ibid.*, liv., p. 484.
- (9) Ueber die elementare Zusammensetzung des Ochsenfleisches. *Ibid.*, lv., p. 345.

E. H. STARLING.

THE EVOLUTION OF IGNEOUS ROCKS.

THE labours of many workers during the thirty years which have elapsed since the revival of petrological study are already bearing fruit, and geologists in general are not slow to perceive the value of the new data already at their disposal with reference to some of the more difficult problems of their science. Indeed, it is not too much to say that from the purely descriptive study which has been content to describe itself as petrography, there is already emerging a philosophy of petrology, which, we may expect, will soon be able to deal successfully with very broad questions. Of these questions none is of greater interest or more fundamental importance than that of the origin and mutual relations of igneous rocks.

The day is past when a writer was content to describe a rock as consisting of certain specified minerals, and thought, for instance, that he sufficiently accounted for a high silica-percentage in an analysis by stating that the rock contained free quartz. It is recognised that, in a rock formed from igneous fusion, the chemical composition must be in general the prime datum; so that it is not the minerals that form the rock, but the rock (or rather the rock-magma) that forms the minerals. Petrologists have thus been led to discuss the physics and chemistry of the molten magmas, by the consolidation of which igneous rocks have been formed, and, in particular, to inquire how such diversity could arise in the composition of these magmas as is proved by the great variety observed among the resulting rocks. If we grant, as is conceivable and indeed probable, that a rock can be formed from a magma of different composition from its own, the conditions under which this might take place open up a new branch of the problem.

It has long been known that igneous rocks of widely different chemical (and in part mineralogical) composition often occur in close association, and many facts seem to

indicate that very different magmas may be derived from the same ultimate source. Taking first volcanic rocks, it is noteworthy that though the lavas erupted at different times within one volcanic district may differ widely in chemical composition, ranging sometimes between very acid and very basic types, yet there are often striking chemical peculiarities which run through the whole group of rocks belonging to one volcanic centre, differentiating them from those of other centres, and only to be explained by some kind of *consanguinity* among the associated lava-flows. This is well brought out in a paper by Iddings,¹ in which he reviews the general subject of the origin of igneous rocks, and draws illustrations especially from those studied by him in the Yellowstone Park region. These are discussed under three heads. The volcanic rocks of Electric Peak and Sepulchre Mountain range in silica-percentage from 56 to 69, but still have distinctive characters in common, such as the constant predominance of soda over potash, the molecular ratio of the two varying from 3 : 1 to 2 : 1. The rocks of the old volcano of the Crandall basin show a greater range of composition, the silica-percentage being 52 to $71\frac{1}{2}$ in different examples, but they have peculiarities which link them together. The alkalis are here more plentiful, and the predominance of soda over potash less marked, the molecular ratio being between 2 : 1 and 1 : 1. In the peculiar dykes and flows of the Absaroka range, with a silica-percentage ranging from 47 to $69\frac{1}{2}$, the alkalis are present in still greater force, and are about equally represented. Iddings compares these three groups of rocks with those of the well-known Italian volcanoes, also rich in alkalis, and finds that each district has its own chemical characteristics. In the case of Vesuvius the molecular ratio of soda to potash varies from 7 : 4 to 1 : 4. In the Etna lavas the ratio is much higher, rising even to 8 : 1, while lime and magnesia are very abundant. In the peculiar rocks of Pantellaria the ratio is from 5 : 1 to 2 : 1. Here iron-oxides are richly present, and increasingly so in the more acid rocks. Iddings shows these various relations graphically, taking the molecular numbers of silica as

abscissæ and those of the various bases as ordinates for their respective diagrams.

Attempts have been made to verify directly the change in the material erupted by a single volcano through long periods. Lang² has critically examined the cases of Vesuvius and Etna, for both of which we have a large number of chemical analyses, even when the older ones, conducted with imperfect analytical methods, are eliminated. Fuchs had already concluded (1870) that, in spite of the complex and peculiar mineralogical constitution of the Vesuvian lavas, the chemical composition of the different flows erupted in historic times is almost exactly the same; and von Lasaulx (1880) had arrived at a very similar conclusion for the Etna lavas. Lang, however, makes a more searching examination of the analyses, laying special stress on the relative proportions of lime, soda, and potash given by the bulk-analyses of the several rocks. From a discussion of fifty-five trustworthy analyses of different lavas of Vesuvius, he finds that their mean composition for different periods of fifty years does vary sensibly, and, in particular, that the lavas of 1740 to 1790 were richer in alkalies and silica, and poorer in lime than those which preceded and followed. This variation, however, is not great, and is evidently not progressive. He also notes during each period a slow variation which does appear to be progressive: thus the lavas of the last hundred years show on the whole a gradual increase in the proportion of lime and a corresponding falling off in potash. Again, in the Etna lavas from 1766 to 1879, the author points out a gradual increase in lime as compared with the alkalies, the ratio rising progressively from 1.36 to 2.88. Despite the small variations noted, the general impression obtained from Lang's tables is that of remarkable constancy in the composition of the lavas from one vent through many centuries: for instance, the silica-percentage of the rocks poured out from Vesuvius has scarcely changed since the days of Pompeii. The conclusion is that the processes which produce changes act very slowly. By taking thousands instead of hundreds of years, we might expect to find greater

differences. This is indeed illustrated in the special districts in question: the Etna lavas here discussed are very distinctly more basic than the older volcanic rocks connected with the same centre.

In such volcanic districts as have been carefully studied, a definite order of succession in time has been observed for the different types of lavas erupted, and this order, despite exceptions, seems to be a significant one. In numerous cases the law seems to be that the earliest products are of intermediate chemical composition (andesites, etc.), while the later ones become progressively more acid, or more basic, or both alternately or simultaneously, *i.e.*, increasingly different from the first. Two recently recorded instances of this apparent *progressive differentiation* may be added to those already well known.

In the Eureka district of Nevada, Hague³ gives the following as the order of the eruptions in Tertiary times: i. hornblende-andesites, ii. hornblende-mica-andesites, iii. dacites, iv. rhyolites, v. pyroxene-andesites, vi. basalts. Here the series i., ii., v., vi. is one of increasing basicity, while i., iii., iv. is one of increasing acidity.

In Mexico,⁴ again, the Tertiary eruptions began in the Upper Miocene with what are described as andesitic porphyrites and propylitic andesites, and these were followed by extensive outpourings of hornblende-andesite. In Pliocene times there followed in order: hornblende-mica-andesites, hornblende-hypersthene-andesites, hypersthene-andesites, augite-andesites, and labradorites, the last graduating into the numerous basaltic flows which have continued through Quaternary times. Here the general order is one of increasing basicity, but the acid series is also represented, though with less completeness. Rhyolites occur, of which the precise epoch is not known, but is later than that of the hornblende-andesites.

The initial magma cannot be assumed to have been in every volcanic district one of intermediate composition. In Iceland, for example, is found an enormous extravasation of basic material, while the intermediate and acid lavas are much more scantily represented. Still rhyolites occur in

numerous localities in the island, and are considered by Bäckström⁵ to be products of the differentiation of an original basic magma. It is worthy of note that they are soda-rhyolites, potash being always subordinate to soda. The intermediate rocks, which occur sparingly, are not typical andesites, but have a more peculiar composition.

The great predominance of basic lavas is observed not only in Iceland, but in Northern Ireland, Western Scotland, the Færöer Isles, and probably a considerable part of the Arctic regions, all of which have belonged in Tertiary times to one *petrographical province*. The existence of such provinces, each having its varied group of igneous rocks agreeing in certain characteristics and differing from the types developed in adjacent provinces, naturally leads to the idea of a differentiation in space as well as in time, and that on a regional scale. Judd long ago pointed out the strong contrast between the Tertiary volcanic rocks of Bohemia and of Hungary, divided by the Carpathian Chain, and the idea can be extended to other parts of Europe. Iddings, in the memoir already cited, remarks that America is divided by the long chain of the Rocky Mountains and the Andes into two vast regions, the igneous rocks of which offer a like contrast. Rocks relatively rich in alkalis occur along the eastern side of the Rocky Mountains, in the Central and Eastern United States and in Canada, in Brazil and along the eastern part of the Andes, in Argentina and Paraguay; while in the western region quite different types are found, the alkali-rocks (*e.g.*, those carrying leucite or nepheline) being, with one exception, unknown there. The Yellowstone Park district lies near the dividing line of these two great regions, and the rocks of the three centres described there by Iddings show considerable differences according to their situations.

It is not a little interesting to observe how regions petrographically different are divided by mountain ranges; the problem of the differentiation of igneous rock-magmas on a large scale seems thus to connect itself with that of crust-movements, but this is an almost untouched field of speculation. Perhaps materials are not yet available for

examining the distribution of the eruptive rocks of greater geological antiquity in Europe in relation to the Hercynian and older mountain ranges.

Although the fact and even some of the laws of differentiation in subterranean igneous magmas might be inferred with considerable probability from a comparison of lavas at the same and at different volcanic centres, the phenomena and possible causes of such differentiation are to be studied especially in rocks which have consolidated under deep-seated conditions, and have been exposed by erosion. Here we find in close association rock-types of widely different chemical composition, but often having peculiarities in common which point unmistakably to their consanguinity, and the relative ages of such associated rocks is indicated by the manner in which the newer cuts through the older. Further, we find not infrequently in one and the same plutonic body of rock petrographical types differing chemically as well as mineralogically, but passing into one another by imperceptible gradations.

An excellent example of such a complex of plutonic rocks is that described by Dakyns and Teall⁶ in the Garabal Hill district, near Loch Lomond. The major part of this area of igneous rocks is occupied by a porphyritic granite. To the east of this occur a non-porphyritic granite and a less acid rock, described as tonalite or quartz-diorite, and then a diorite proper, forming the margin of the complex, especially on its south-eastern edge. Associated with this are patches of ultrabasic rocks (peridotites). The complex thus includes rocks ranging from thoroughly acid to ultrabasic, related to one another in a definite manner. In some places a sharp line can be drawn between adjacent rock-types, and when this is so, the more acid rock is always found to be newer than the more basic; in other places the several types pass gradually into one another. The several magmas were, therefore, introduced in order, beginning with the most basic and ending with the most acid; but the process was in a broad sense a continuous one, and it is irresistibly suggested that the different magmas came from a common source. A series of seven chemical analyses shows in the

successive intrusions a gradual decrease in the proportions of iron-oxides, magnesia and lime, and a corresponding increase in silica, potash, soda, and alumina, the last two declining again at the acid end of the series, which includes members with silica-percentage ranging between the extremes $37\frac{1}{2}$ and 76. These relations are made clearer by reducing the analyses to molecular ratios and plotting them graphically after the fashion of Iddings. An examination of the constituent minerals of the rocks, taken in the same order, leads to equally interesting results. The more basic silicates disappear in turn, while more acid ones come in, the order thus arrived at being as follows: olivine, pyroxene, hornblende, biotite, plagioclase, orthoclase and quartz, microcline. Now this is also the order of crystallisation of the several minerals in so far as they occur together in the same rock, or, more accurately, it is the order in which the several minerals began to crystallise out from the magma, for their periods of crystallisation to some extent overlapped. This order, as Rosenbusch has remarked, is the normal order in plutonic rocks in general, and may be roughly summarised as an order of decreasing basicity. Our authors point out that the earliest intruded rocks are thus the rocks richest in the earliest formed minerals. If this is to be regarded as a fact of general significance, it seems to point to a connection between crystallisation and differentiation in the presumed parent-magma. Such a supposition might be fortified by evidence from other districts, where the law of the more acid rock cutting the more basic seems to hold very widely.

In this connection we may note in passing the observation of Bayley⁷ on the great mass of gabbro in North-eastern Minnesota. This remarkable body of rock exhibits striking variations in composition in different parts, being sometimes very rich in olivine, sometimes rich in augite and biotite, and again poor in augite and very rich in feldspar. Nevertheless, so far as the investigation goes, the feldspars of these various types seem to be of practically the same variety, a basic labradorite. If the differentiation had been effected in the magma prior to the crystallisation of the

felspar, we should expect the different partial magmas to have given birth to different varieties of felspar. There are, however, in other districts, examples of plutonic rocks apparently derived from a common source, but differing widely in *mineralogical* as well as in chemical composition. In such cases it must be supposed that differentiation was, at least in the main, anterior to and independent of crystallisation.

This and other very interesting points are illustrated in a recently published paper of Brögger⁸ on the rocks of Gran near Christiania. Intruded in Devonian times among the older strata of the Christiania district, there occurs a group of igneous rocks ranging from very basic to acid, but having in common certain peculiarities, such as an unusually high content of soda, which would alone afford strong presumptive evidence of consanguinity. The field-relations of the rocks are equally convincing on this point, and further bring out the fact that the succession in time of the several types is a definite one, *viz.*, an order of increasing acidity. The whole group of rocks has been interpreted by Brögger in former memoirs as the products of successive intrusions from a large subterranean magma-reservoir, in which differentiation had already taken place. Such magma must have underlain a large tract of country, and may itself have originated by differentiation on a regional scale from a hypothetical magma of much wider extent. This paper deals only with the earliest and most basic product of differentiation of the general magma of the Christiania district, and the author shows that this in turn underwent differentiation within the limited area described in the vicinity of Gran. The rocks in question occur along a tract some thirty-three miles long, following a line of fissure which runs roughly north and south. The dominant type is described as an olivine-gabbro-diabase, but it is pointed out that its chemical, and in part its mineralogical, composition varies in a definite manner in the different exposures, the silica-percentage increasing from 43.65 in the north to 49.25 in the south. This is taken to indicate a differentiation of the basic magma on a rather

large scale. Besides the dominant rocks, there are along the whole stretch of country innumerable dykes and sills. These are of two peculiar rock-types, camptonite and bostonite, the one more basic, the other more acid than the olivine-gabbro-diabase. The two are intimately associated, often in the same dyke-fissure; but where one cuts the other, the bostonite is invariably the newer. The field-evidence proving that these dykes are genetically connected with the main basic intrusions, Brögger regards the two rock-types as *complementary* products of differentiation of the original basic magma, and he shows from the analyses that nine parts of camptonite and two of bostonite give almost precisely the mean composition of the olivine-gabbro-diabase. This differentiation must have been effected prior to crystallisation of any importance, as is clear from the striking difference in mineral constitution between the rocks: for instance, the ferro-magnesian minerals in the main intrusions are olivine, pyroxene, and biotite; in the camptonite dykes, brown hornblende. Camptonites and bostonites are known in other countries, such as Canada, in connection, not with gabbro, but with nepheline-syenite, and we learn that the same rock-types may arise by differentiation from more than one kind of parent-magma. Again, the large masses of olivine-gabbro-diabase are found to pass frequently into special basic rocks, such as pyroxenites, which are traversed by segregation-veins of a more acid rock, akerite or augite-syenite. These types also are regarded as complementary products of differentiation from the original basic magma, and it thus appears that a given parent-magma may be differentiated into partial magmas in more than one way, with different results.

As an example of differentiation of a totally different kind, we will take the case of certain muscovite-biotite-gneisses in the highlands of Forfarshire, the peculiarities of which have been described by Barrow.⁹ The field-relations of these rocks conclusively prove their igneous origin and intrusive nature. They form innumerable thin sills, bands, and veins in rocks highly metamorphosed by them, and

they have evidently been injected under great pressure. They consist essentially of oligoclase, muscovite, biotite, quartz, and subordinate microcline. Apart from the gneissic structure, which is not constant, they differ from normal granites, chiefly in their smaller proportion of potash-felspar and quartz and in a peculiar rounded form of the crystals of oligoclase. The micas, which crystallised earlier, are well shaped, but the oligoclase, which came next, seems to have been arrested in its growth before the crystals attained their proper form. It resembles, indeed, the rounded nucleus so frequently outlined in the feldspars of normal granites by zones of growth, but completed there by an outer shell with crystal contours. What happened then to interrupt the normal course of consolidation when the oligoclase was but partially crystallised out? The answer seems to be that at this stage the residual liquid was in part drained off and squeezed forward (in a southerly direction) as a partial magma richer in potash and silica than the original magma. It is now found consolidated in the form of pegmatite. Tracing the gneiss southward, it is found to change character. The oligoclase becomes less rounded and forms a smaller proportion of the rock, the gneissic structure is lost, and muscovite begins to predominate largely over biotite. The rock is now permeated by strings of coarse pegmatite, consisting essentially of microcline, quartz, and muscovite, and this increases in bulk until a massive fringe of pegmatite forms the southern border of the gneiss area. Barrow concludes that in this area a normal granite-magma was intruded in connection with the great crust-movements which have affected the whole region, and was injected under enormous pressure into every fissure and line of weakness in the solid rocks. This was effected concurrently with the progress of crystallisation in the magma, and the liquid portion was thus able to enter crevices too small to admit the already crystallised minerals, and so to travel always in advance. The final residual magma crystallised as pegmatite, and the gneiss and pegmatite, are thus complementary products of the original magma. Differentiation has here been brought about by

purely mechanical forces operating on a magma in which crystallisation was in progress.

This leads to a few remarks on the possible causes of differentiation in rock-magmas, on which question various speculations have been advanced. When the separation is merely between crystallised minerals and the residual magma, it is easy to see that the cause may be a purely mechanical one. We have seen an illustration in the filtering process described by Barrow, and this is of special interest as supplying a possible link between differentiation and crust-movements. Again, gravity must be taken into account as a probable factor. Very little is known regarding the relative densities of rock-magmas and crystals at very high temperatures; but it is to be expected that the more basic minerals at least would sink in a magma from which they had crystallised out, unless that magma possessed a high degree of viscosity; and even in this case, if the viscosity followed the laws laid down by physicists, the sinking, though slow, would be no less certain. Such a process would give rise, in the lower layers of a magma-reservoir, to a relative richness in the more basic minerals. We have seen, however, that in some well-established cases differentiation was certainly not posterior to the crystallisation of these minerals, and geologists have accordingly turned their attention especially to possible causes of differentiation by diffusion in a still fluid magma.

Here again the question of viscosity would seem to be an important one, and any experimental results bearing on the viscosity of rock-magmas are of value. Vogt's¹⁰ researches on artificial slags are of especial interest. They were made on slags having the general composition of rock-magmas, without water or any special fluxes, and under atmospheric pressure. Vogt found that the viscosity of such a slag increases with its content of silica, and increases rapidly if the silica exceeds 58 or 60 per cent., *i.e.*, in magmas corresponding to acid rocks. On the other hand, ferrous oxide in a slag strongly promotes fluidity; magnesia has the same effect, though less markedly; and lime, and probably soda, act in the same sense. A

moderate proportion of potash or a large proportion of alumina in an acid slag produces a notable increase of viscosity. The experiments thus tend to show that a normal acid rock-magma, rich in silica and usually in potash, will be markedly viscous, while a basic one, poor in silica and rich in lime, magnesia, and iron-oxides, will be very fluid. Vogt remarks that the difference between extreme examples of slags is very great: at the same moderate temperature-distance above their respective melting-points, highly basic slags flow like water, while highly acid ones are as sluggish as tar. It is probable that any differences between the slags and natural rock-magmas will favour greater fluidity in the latter, the water which probably forms part of every rock-magma doubtless tending to reduce the viscosity. On the whole, then, we should not expect viscosity to be a serious obstacle to diffusion, at least in the more basic magmas. It is, in fact, in the basic rocks that the actual phenomena of differentiation are most strikingly exhibited.

A not uncommon type of variation in a magma which has been differentiated and consolidated *in situ* is that in which the resulting rocks grow progressively more basic from the centre to the margin of the mass. The phenomena agree with the supposition that those constituents of the magma which are normally the earliest to crystallise out as the temperature falls, *viz.*, the iron-oxides and, in a less degree, the more basic silicates, have become concentrated in the cooler marginal parts of the reservoir. Vogt¹¹ has given an economic interest to this part of the subject by his hypothesis, that certain rich bodies of iron-ore are the products of an extreme "magmatic concentration" of this kind. His results have been abstracted in English, and are well known. Numerous instances of bodies of plutonic rock or dykes becoming more basic in composition from centre to margin have been described by other authors, and several of these are cited in the new edition of Zirkel's text-book.

It is more especially in view of such cases as these that several petrologists have tried to apply what is known as

"Soret's principle". In this view a molten rock-magma is regarded as of the nature of a solution, the constituent which is on the point of crystallising out at any stage of the consolidation being considered as dissolved in the residual liquid, or some special silicate-compound being regarded as the solvent. Now Van 't Hoff's theory of osmotic pressure teaches that if different parts of an ordinary saline solution be at different temperatures, the concentration will also vary, equilibrium being attained only when the concentration in different parts is inversely as the absolute temperature. Experiments tending to the same general conclusion had previously been made by Soret. This idea, applied to rock-magmas, has been held to afford some explanation of the relative concentration of the basic constituents in the cooler part of a magma-basin. These constituents, which are the first to separate out when crystallisation begins, are regarded as the least soluble.

The applicability of Soret's principle, at least in its simple form, to the case of rock-magmas has been doubted in various quarters. It is easy to see that the case of a silicate-magma is much more complex than that of a single salt dissolved in water, and in dilute solution. Bäckström,¹² in particular, has adversely criticised the theory, and prefers to the analogy of a saline solution that of a mixture of liquids. Taking an example, he remarks that water and aniline, if mixed at ordinary temperatures, separate into two layers, one consisting of water with about one per cent. of aniline, the other of aniline with about two per cent. of water. If the temperature be raised, the proportions of aniline in the former layer and water in the latter increase, until at 166° the distinction between the two layers disappears. This property of mixing freely above a certain temperature, and separating more and more completely as the temperature falls below that degree, is, he maintains, a property common to all liquid-mixtures where no chemical action takes place; and he proposes to apply it to the case of fluid rock-magmas regarded as mixed liquids.

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VERMES, CŒLENTERA AND PROTOZOA.

ALTHOUGH there are no very startling discoveries to record either in the anatomy or development of the lower groups of Invertebrates, we may consider that, on the whole, very steady progress has been made.

Those investigators who devote their energies to these lowly creatures have been filling up the gaps in our knowledge of the anatomy and development of some of the most important and interesting genera, or in completing, so far as possible, the account of their distribution over the face of the globe. Several new genera and species have been described, the number being considerably larger in the groups of parasitic worms and protozoa than in the Cœlentera, but no new forms of any very striking morphological importance have come to light; nor have any considerations, based upon anatomical or embryological research, been brought forward, which would justify any serious alterations in the classifications that are usually adopted.

The most important monograph dealing with special genera is that of the late George Brook, on the genus *Madrepora*, published by the trustees of the British Museum. This valuable work contains an account of no less than 220 species, and is fully illustrated by 35 quarto plates of collotype reproductions of photographs taken by the author.

A careful and conscientious monograph such as this is cannot fail to be of great use to those who wish to identify species; but it is greatly to be regretted that the author's life was not spared to give us a condensed summary of the known facts concerning the geographical and bathymetrical distribution of the genus.

Before the publication of Brook's monograph, Rehberg had published¹ some useful lists of the names of the species of *Madrepora* occurring on the coral reefs of different regions

¹ Rehberg, H., *Neue und wenig bekannte Korallen*, *Abh. Ver. Hamb.*, xii., pp. 1-50.

of the world; but had he had the advantage of working with the help of this new monograph, his lists would have been much more complete and useful than they are. Now that we have so much knowledge of the species of *Madrepora*, it is to be hoped that some naturalist will before long undertake the task of giving to us a monograph of the distribution of this important and interesting genus.

Leaving, for the present, matters connected with the progress of our knowledge of the systematic zoology of these groups, and passing on to recent anatomical and embryological research, we find that among recent papers one of the most important is that of Harmer, on the "Embryonic Fission in the Cyclostomatous Polyzoa".¹

Several examples of a process of fission or gemmation of very young embryos or embryonic forms have been known to naturalists for some little time. One of the best known of these is the case of the earth-worm *Lumbricus trapezoides*, investigated by Kleinenberg, where the embryo, whilst still in the gastrula stage, either divides into two equal halves, each of which produces a complete embryo by simple fission, or produces two or more buds by a process of gemmation.

The production of lateral buds on the *Scyphostoma* or larval hydra-tuba stage of certain jelly fish belonging to the order of *Scyphomedusæ* may be regarded as belonging to the cases of embryonic gemmation, but an even earlier form of this occurs in *Chrysaora* and *Aurelia*, in which, as Busch and Haeckel have shown, numerous buds may be formed by the larvæ whilst still in the gastrula stage.

These facts then prepare us for an account of embryonic fission or gemmation in a group of animals, such as the Polyzoa, which multiply during their lifetime very rapidly by the ordinary processes of asexual reproduction.

The subject of the investigation was *Crisia ramosa*, a species which is common in the water near Plymouth. On the examination of the growing point of a branch of

¹ Harmer, S. F., Embryonic Fission in Cyclostomatous Polyzoa, *Quart. Jour. Micr. Sci.*, xxxiv.

the colony, Mr. Harmer found that certain buds may be distinguished at an early stage from the ordinary buds which form the polypides of the Zoëcia, by the fact that each of them contains a single large cell or ovum. These buds, separated off from the true growing point by ordinary septa, and homologous with the Zoëcia, become modified to form the structures which are, rather unfortunately, called the ovicells. Each "ovicell" is, in fact, a chamber, in protoplasmic communication with its neighbours, largely filled up with ordinary funicular tissue, but containing an obvious polypide bud and one ovum. The process of fertilisation was not observed, but there can be little doubt that it takes place. The segmentation is remarkable for the fact that the blastomeres are either very loosely connected with one another or quite separate, a condition which is only paralleled by the cases of *Salpa*, as described by Salensky, and *Dendrocœlum*, as described by Halley. This is followed by the formation of an embryo, in which it is difficult to distinguish any definite embryonic layers, as it consists of simply an undifferentiated protoplasmic mass in which nuclei are irregularly scattered. After a time this embryo sends out several finger-shaped processes, each of which becomes divided up into rounded masses of cells by a series of transverse constrictions, and each of these rounded masses of cells becomes a larva.

Although this interesting process of embryonic fission has only been observed in this one case of *Crisia ramosa*, it is not improbable that future investigation will prove that it is of common occurrence among the Cyclostomatous Polyzoa.

Among the notable papers of recent times, one by Dr. Fowler¹ on the anatomy of *Rhabdopleura* must be referred to. A renewed investigation of this interesting form has led the author to the conclusion that it must be included with *Balanoglossus* and *Cephalodiscus* in the group of the Hemichordata. It is some years now since Bateson

¹ Fowler, G. H., "Morphology of *Rhabdopleura Normani*," Leuckart's Fest., 1892.

pointed out that *Balanoglossus* possesses, in addition to its vertebrate character of pharyngeal gill slits, a small structure projecting from the dorsal wall of the pharynx into the proboscis, which histologically and morphologically resembles the notochord. For this and for other reasons, which it is not necessary to discuss here, he proposed to establish a group called the Hemichordata for the reception of *Balanoglossus*, in order to indicate more clearly its supposed chordate affinities.

A few years later a remarkable colonial animal was discovered among the material brought home by the Challenger expedition, which was at first supposed to be a Polyzoan, but was afterwards proved by Harmer to possess a notochordal structure similar to that of *Balanoglossus* and a single pair of gill slits. *Cephalodiscus*, as this animal was called, was, therefore, transferred to the Hemichordata.

The genus *Rhabdopleura* has occupied for many years a very uncertain position in our systems of classification. It forms creeping colonies, which are found attached to ascidian tests and dead corals in deep water in the Norwegian and Scotch fjords. Discovered by the Rev. A. M. Norman, in 1868, it has been the subject of memoirs by Profs. Allman, Sars, and Lankester, but it was left for Fowler to discover the existence of a notochord similar to that of *Balanoglossus* and *Cephalodiscus*, and to point out other features in which it shows affinities with the Hemichordata. In one important respect, however, it differs from these other two genera, and that is in the absence of gill slits. Whether this is a character, which in itself should be considered sufficient to separate *Rhabdopleura* from the Hemichordata, is a question which cannot be satisfactorily answered until we have some account of its development, but it is a great gain to know at last in what direction its true affinities lie.

The two great groups of parasitic platodes—the Trematoda and Cestoda—are separated from one another by several anatomical characters; but, of these, the two most obvious and important are that, whereas the Trematoda

are unsegmented animals, with a well-marked alimentary canal, the Cestoda are divided by a number of constrictions into a series of segments, and possess no trace of an alimentary canal. When, therefore, we find a parasitic platode that has an unsegmented body and no trace of an alimentary canal, we are naturally anxious to learn whether its affinities are more closely connected with the former group or the latter. Such an animal is *Caryophyllæus*, a form that is found parasitic in the intestines of a certain fresh-water fish.

We are indebted to Dr. H. Will¹ of Retelsdorf for a careful study of the anatomy of *Caryophyllæus mutabilis* parasitic in the intestines of the bream of the Warnow River, and for a very strong confirmation of the views previously held by most naturalists that this interesting parasite, although showing some primitive features, is, nevertheless, a true Cestode.

The principal points brought out by Will's paper are briefly as follows: The excretory system is in very marked contrast to that of most of the Cestodes. It consists of four main ascending trunks, which collect the secretion of capillaries from the parenchymatous tissues of the body, and pass forwards from the trunk towards the head. In the region of the neck these four trunks unite into two, which in the head break up into a complicated anastomosis. Passing backwards from the cephalic anastomosis are ten descending trunks, which unite together at the excretory pore, situated at the posterior end of the body.

In the arrangement of the single group of sexual organs, *Caryophyllæus* approaches that of the *Bothriocephalidæ*, a family which many naturalists consider to be more primitive in their anatomy than the true tapeworms. In the *Taeniadæ* the uterus is a branched organ, which communicates only with the genital pore by the vagina. In the *Bothriocephalidæ*, on the other hand, the uterus communicates with the exterior by a separate *os uteri*, situated some distance apart

¹ Will, H., "Anatomie von *Caryophyllæus mutabilis*," *Zeitschr. f. wiss. Zool.*, lvi. 1.

from the generative pore. In *Caryophyllæus*, although there is, as in the *Bothriocephalidæ*, a separate vagina and uterine duct, these join together and open at the generative pore as a single duct.

But perhaps the most important part of Will's work lies in his account of the nervous system. He finds in the trunk ten nerve cords running longitudinally down the body. Of these, two run laterally within the longitudinal layer of muscles, and are considerably larger than the others. These he calls the principal trunks ("hauptstämme"). Of the remaining eight, all of which run outside the circular muscular layer, two are situated dorsally, two ventrally, and four laterally. The four lateral nerves of the outer layer are situated close to the principal trunks, although separated from them in the body region by a thin layer of muscles, but in the region of the neck they fuse with them; so that there only six trunks in all can be seen in transverse section. In the head, the six lateral nerves break up into a complicated anastomosis, in which may be recognised two principal ring commissures, and twelve main cephalic nerves.

In other Cestodes, such as various species of *Taenia*, *Acanthobothrium coronatum*, etc., ten longitudinal nerve cords have been described, two principal trunks and eight smaller accessory ones. In the group of the Trematoda, on the other hand, only six lateral nerves have been recognised, of which the two ventral are the thickest and most important. Will considers, after a careful examination of the histology of the nervous system, that the four lateral accessory nerves of *Caryophyllæus* ought to be considered part of the principal lateral trunks, and, consequently, that the nervous system of *Caryophyllæus* shows greater affinities with that of the Trematodes than with that of the Cestodes. *Caryophyllæus* then must remain among the Cestoda, but in the simple unsegmented form of its body, in the arrangement of the sexual organs, and in the character of nervous system it is more primitive than the other tapeworms.

Considerable interest has been aroused recently by a controversy which has been going on for some time past

between two distinguished German naturalists, as to the systematic position of the Scyphomedusæ. No one who has studied this group at all carefully can doubt for a moment the justification of the step that was taken by the older naturalists in separating the "covered-eyed" medusæ from the "naked-eyed". In many anatomical characters, such as the absence of a velum, the endodermic origin of the gonads, the presence of gastral filaments, and the structure of the sensory bodies, the covered-eyed medusæ, or Scyphomedusæ as they are now called, are widely separated from the naked-eyed medusæ, or Hydromedusæ. But to remove them from the Hydrozoa altogether, as Goette wishes us to do, and place them in the class Anthozoa, is a step which cannot be taken without very careful consideration of the facts of anatomy and development.

The main point upon which the whole controversy turns is the presence or absence of an ectodermic invagination in the developing larva which forms the lining epithelium of the manubrium and a part of the gastric cavity. Unfortunately, upon this point we find very divergent statements.

Claus¹ has recently published a paper in which he maintains that the inner lining of the manubrium of the Scyphomedusæ is not formed from the ectoderm at all but from the endoderm. He carefully reinvestigated the development of the two genera *Chrysaora* and *Cotylorhiza* at the zoological station at Trieste, and found that the place where the ectoderm and the endoderm join is the edge of the mouth. From this it follows that the gonads, the gastral filaments, and the epithelium of all the gastric pouches are of endodermic origin, and there is nothing in the structure of the Scyphomedusan which corresponds with the stomodæum of the Anthozoa. The temporary ectodermic invagination which takes place at the distal pole after the free swimming gastrula embryo comes to rest is again evaginated to form the proboscis

¹ Claus, C., Ueber die Entwicklung des Scyphostoma von *Cotylorhiza Aurelia*, und *Chrysaora*, *Arch. z. Inst. Wien.*, x.

or manubrium. The results obtained by Claus are in accordance with those of Playfair McMurrich,¹ who, working quite independently of the German professor, discovered no trace in the development of *Cyanæa arctica* of an ectodermic stomodæal invagination.

Since the publication of the results obtained by Claus and McMurrich, Prof. Goette of Strasburg has again entered the field, and in the description he gives of the development of *Cotylorhiza* and *Pelagia* confirms his previous statements as to the existence of an ectodermic stomodæum in the *Scyphomedusæ*.² Without reference to or comment upon the results obtained by Claus and McMurrich, Prof. Goette describes the formation of an ectodermic stomodæum and an œsophageal perforation or "Schlundpforte" connecting the stomodæum with the cœlenteron. He goes further than this, however, and declares that the second pair of gastral pouches and all its derivatives are also formed by the ectoderm. The gonads and gastral filaments of the adult medusæ may, however, occur in all the pouches; consequently some of them must be of ectodermic and others of endodermic origin, a conclusion which would entirely upset the importance of the place of origin of the sexual cells of Cœlenterates, as insisted upon by the Hertwigs and others.

It is not likely that Goette's views on this important point will meet with any very general acceptance until his results have been completely confirmed by independent observers. It is an extremely difficult matter in studying the development of many forms of Cœlenterates to determine with any degree of certainty where the ectoderm cells end and the endoderm cells begin. There is very seldom any abrupt limit between the two germinal layers at the points where they meet, and, as Goette himself admits, in the *Scyphomedusæ* the layers are connected

¹ McMurrich, J. P., The Development of *Cyanæa arctica*, *Am. Nat.*, 1891.

² Goette, A., Vergleichende Entwicklungsgeschichte von *Pelagia noctiluca*, *Z. f. wiss. Zool.*, lv., p. 645.

with one another by a number of cells of an intermediate character. Goette's figures, too, are by no means convincing that what he letters ectoderm is not really endoderm or *vice versâ*.

The controversy is an interesting one, and will doubtless be carefully followed by those who are studying this group of Cœlenterates, but it is not possible to say at present that very much progress has been made.

Passing on to the group of the Protozoa, we find very few papers that have excited very general interest. The well-known eye spots of the Flagellata have recently been subjected to a careful examination by Franzé.¹ Each of these organs consists of a mass of pigment of various shapes, and one or more transparent lens-like bodies, lying in or on it. A careful study of the chemical reactions given by these lenses shows that in some cases, such as the Euglenidæ, they are composed of paramylum; and in others, such as the Chlamydomonads and Volvocineæ, they are composed of amylum. Their development is dependent upon the metabolic activity of the organisms, and the author found that after Euglenæ had been kept in the dark for some time, the size and number of their lenses were considerably reduced. This he attributes to the diminished metabolic activity in the dark of the chlorophyll bearing Flagellates. He also observed that those species of Euglena which naturally possess few paramylum granules show either no lenses or very few in their clear red eye spots.

As a great deal of attention has been paid recently to all matters dealing with the minute structure, and the phenomena accompanying the division of the nuclei of cells, Rhumbler's² account of those curious bodies, usually considered to be nucleoli, which occur in the nuclei of many Protozoa, will be read with much interest.

¹ Franzé, R., *Zur Morphologie und Physiologie der Stigmata der Mastigophoren*, *Z. f. wiss. Zool.*, lvi., part ii.

² Rhumbler, L., "Ueber Entstehung und Bedeutung der in den Kernen vieler Protozoen und in Keimbläschen von Metazoen vorkommenden Binnenkörper (Nucleolen)," *Zeitschr. f. wiss. Zool.*, lvi., part ii.

In a great many Foraminifera, he finds a considerable number of small irregular bodies lying in the substance of the nucleus. They are sometimes spherical in shape, sometimes angular and pointed, frequently collected together in grape-like clumps. Another feature common to them is their extreme irregularity in number; in the arenaceous Foraminiferan *Saccamina sphærica*, for example, they vary from 1-300 in number. Similar structures have been described by Hertwig in *Thalassicola*, by Stanley Marshall in certain Gregarines, and by several observers in the germinal vesicles of ova.

Rhumbler considers that the changes in their shape, and the way they react to staining fluids, proves that they are not really organised structures, but are due to the accumulation in the substance of the resting nucleus of organic substances, which are at first fluid, then become viscid, and eventually solid. Their extreme irregularity in occurrence, some nuclei being apparently quite devoid of them, and their disappearance before karyokinetic changes commence, lend very strong support to Rhumbler's views. There can be little doubt that they are not of the same nature as the well-known chromatin bodies, or that they are not directly converted into them, but whether they are, as it were, stores of proteid food material, by which the chromatin bodies are nourished during their rapid growth at the commencement of Karyokinesis, is a question which it is at present very difficult to decide.

A great deal of good work has recently been done in the group of parasitic Protozoa—the Sporozoa, more particularly in their relation to disease, but as an account of these researches would lead us beyond the limits assigned to this article, a consideration of them will be left for the next number of this journal.

SYDNEY J. HICKSON.

ON THE STUDY OF ADAPTATION IN PLANTS.

THERE are two characteristics which are apparent in plants and animals: firstly, the organisation and division of labour in general which they exhibit; and, secondly, their adaptation to their environment. It was natural to begin by studying the former problem first, and only to attempt the solution of the second later on. But during the last few decades this aspect of botany has attracted an increasingly large share of attention, and various causes have contributed to this result. The researches of former times had enabled us to arrive at certain definite conclusions on the subject of the external and internal construction of plants, so that the simple enumeration and addition of new facts in this direction no longer attracts so wide an interest. But the great problem of the future—the investigation of the qualities of protoplasm—seems for the present to afford but little prospect of solution. If we may use a metaphor, we might say that Botanical Science is like a mountaineer, who, after long weary climbing, only discovers that after all there still rises—steep and apparently impossible to scale—the real peak; but, notwithstanding this, on casting his eyes around, he finds himself well rewarded for the toil he has undergone. It was particularly by following the stimulating example of Darwin in his researches on the Pollination of Orchids and other plants, his works on climbing and on insectivorous plants, that we have been enabled to see the biological meaning of many arrangements which had either been little observed or entirely misunderstood, and have begun to grasp the meaning of adaptation in the struggle for existence.

As a third reason for the revival of this branch of Botany, I should recognise the fact that during the last few years we have begun to attain to a more accurate knowledge of tropical plants. This was rendered possible by the erection of the first excellently-appointed botanical

station in the tropics by Dr. Treub. Our European flora is but a small—we may even say, a miserable—fraction of the whole. But it is just that fraction in Botany which has been developed, and thus it happens that our judgment on the organic formation of plants is frequently but one-sided and European. Two examples may serve to illustrate this: among our native ferns, if we except the seedling stage and the scale-leaves of the *Osmunda* and *Struthiopteris*, we only recognise a difference in the development of the leaves to the extent that the form of the sporophylle differs from that of the foliage leaves. Among the tropical ferns some have long been known which, in one and the same specimen, produce leaves of strikingly diverse appearance; amongst these are a few species of the genus *Polypodium* (section *Drymaria*), and the remarkable genus *Platynerium*. Regarding these from the standpoint of our knowledge of native ferns it was stated in all descriptions, and, as systematists are usually very conservative, it will probably long be affirmed, that there exists here only a difference between sterile and fertile leaves. My observations made in Ceylon and Java¹ have shown, however, that such is not the case. Sterile and fertile leaves are, on the contrary, formed quite alike in the above-mentioned ferns. But amongst the sterile ones the effects of division of labour become apparent. Most of them are suited, in a manner of which we have no example among our native ferns, for the performance of functions which are connected with the epiphytic mode of life of those ferns just mentioned. Thus *Polypodium quercifolium*, *Polypodium diversifolium*, and others, have leaves which form ledges or pockets upon the stem of the tree on which they grow and in the pockets; humus formed from fallen leaves, pieces of branches, etc., collects and is absorbed by the roots of the fern, thus enabling it to attain to its great size.

Some species of *Platynerium* possess gigantic pocket-forming leaves, others—such as the frequently cultivated *Pl. alcinorne*—form humus by the rapid decay of their

¹ Cf. Goebel, Pflanzenbiologische Schild., 1889-1893.

leaves, which fold over each other like the leaves of a book. A further example is also seen in the *Utricularias*. The only forms which occur in Europe are aquatic plants, and which have long attracted notice on account of their bladders which serve as traps for small animals. But the biology of the whole plant, and the meaning of its separate parts, was not evident till it became possible to examine the mode of life of their numerous congeners.¹ Many of these are terrestrial species, and it appeared—incredible as it may perhaps seem to many—that the *Utricularia* plant—as represented in the European forms—corresponds to one leaf. But if any one doubts that such a far-reaching change in the development of a leaf, an adaptation of functions so widely divergent from the general rule, can possibly occur, the explanation of his position is to be sought in the relatively commonplace character of our native flora. If, on the contrary, we look at the tropical plants, we find among them some whose leaves penetrate into the ground, and function as roots, serving as organs to keep the plant firmly attached to the substratum and to absorb nourishment from it,² and on the other hand there are others whose roots resemble leaves and actually subserve their functions (*Dicrca*, *Taniophyllum*, etc.).

The researches on adaptations have taken two directions. In the first place, it was necessary to settle which structural conditions were to be regarded as adaptations, and, in the next place, the question arose: How do adaptations primarily occur? In other words, there was an effort made to formulate a *theory of adaptation*. Let us first look more minutely into the facts, and select some of the more important advances, which, however, can only be somewhat briefly discussed. All adaptations are either *social*, i.e., they refer to the condition of other organisms, or else *physical*, and are connected with the conditions of life under which nourishment, growth and metabolism take

¹ Cf. *Utricularia* in *An. du jard. botan.*, d. Buitenzorg, vol. ix., and *Pflanzenbiol. Schild.*, ii.

² Cf. Zur Biologie, v. *Genlisea*, *Flora*, 1893, p. 208.

place. Besides these, however, there are further adaptations to be taken into consideration which concern the characters of the organs and tissues, as well as those which result in the exhibition of irritability, or in responsive action to a stimulus.

In both cases a study of adaptations has often led to erroneous conclusions. For in order to understand them aright we must possess precise and accurate knowledge on two distinct subjects. First, the *conditions of life* of the plant; this alone, however, will not suffice, there must be at our disposal, secondly, the results of investigations on the comparative morphology of kindred plants, a side of the question to which I shall revert below.

Among the social adaptations the ant-plants have attracted special attention.¹ Thomas Belt deserves the merit of having first recognised that ants play an important part in the lives of some South American plants, which are constantly inhabited by those insects. I refer to certain species of *Cecropia*, characterised by their hollow and remarkably constructed internodes, in which the ants live, attracted and retained there by the food-bodies which are situated at the basis of the leaves; there are also some *Acacia* whose hollow thorns are inhabited by ants, and food is provided for them at the expense of the plant. Belt's statement that the ants sheltered by these plants serve the latter as a protecting army against the devastations of the leaf-cutting ants has been fully confirmed. And the number of plants which either harboured ants, or attracted them by extra floral nectaries, has been

¹ Belt, *The Naturalist in Nicaragua*, 2nd edition, London, 1886. Among other works on ant-plants I should quote: Beccari, *Piante ospitrici della Malesia e della Papuasie in Malesia*, ii., 1886. Delpino, *Funzione myrmecofila nel regno vegetale*, iii. theile, Bologna, 1886-1889. Treub, *Sur le Myrmecodia de Java*, *Annales du jardin. bot. d. Buitenzorg*, vol. vii. Bower, *On Humboldtia laurifolia as a myrmecophelous plant*, *Proc. Phil. Soc. Glasgow*, xviii. Schumann, *Einige neue Ameisen pflanzen*, *Pringsheims Jahrb.*, xix. Schumann, *Ueber africanische Ameisen pflanzen*, *Ber. der deutschen botan. Gesellschaft*, 1891, heft ii. Wettstein, in *Sitz. Ber. der Wiener Akad. math.-naturw. Classe*, xcvi. bd., p. 568.

vastly increased.¹ And it has been frequently assumed that in all these cases there is a social or symbiotic relation existing between the plants and the ants. Particularly is this the case with those remarkable epiphytic Rubiaceæ, *Myrmecodia* and *Hydnophytum*, described by Rumphius, and which always harbour large numbers of ants in the numerous cavities of their tubers. Beccari recognised in this a marked case of symbiosis, stating that the tubers only arose in consequence of the effect which the ants exercise on the young plant! But no one hitherto has been able to trace the enemies against which the *Myrmecodias* are protected by their guests, and there are no leaf-cutting ants in the districts where *Myrmecodias* grow. The examination of a fern inhabited by ants, such as the *Polypodium sinuosum*, shows² that the hollows, which the ants inhabited, originated from the disappearance of a watery tissue, in which water is stored up for reserve. Such a reservoir of water must be especially necessary for epiphytic plants, as it is more difficult for them to constantly obtain it than is the case with terrestrial forms. I have put forward the same theory with regard to *Myrmecodias*, and in this the distinguished botanist Dr. Treub³ agrees with me. He also showed that the ants did not exercise any influence on the forming of tubers. The occurrence of ants in these plants seems to be in this case only incidental;⁴ and if we suggest that they were perhaps useful in former times, it may be said, on the contrary, that we may only legitimately take refuge in such a hypothesis when we can find no other explanation. The suggestion of a botanist to settle a protecting army of ants on our fruit-trees, by means of sweet-tasting matter, in order to destroy caterpillars, shows clearly how

¹ Such cases are seen in several ferns, not only in *Pteris aquilina* but also in some species of *Polypodium*, further in *Platynerium*.

² *Annales du jardin. botanique de Buitenzorg*, vol. vii., p. 18.

³ *Nouvelles recherches sur la Myrmecodia de Java*, *ibid.*, p. 191.

⁴ As also the occurrence of rotifers in the auricles of some Liverworts (*cf.* Ueber die Blattbildung der Lebermoose, *Flora*, 1893).

frequently cautious and critical treatment in these questions may fail.

In physical adaptations the conditions of life in plants have not been sufficiently taken into consideration. It has been concluded, for instance, that, because the leaves of a plant show certain structural arrangements which involve the reducing of transpiration, they must on that account grow in dry situations. In many cases this is true, but in others not. For we meet with exactly the same structural peculiarities in plants which are found in wet and swampy regions; the absorption of the water is rendered difficult, either on account of the saline properties of the liquid, or the low temperature of the soil.¹ We have some very striking instances of the last fact among our native marsh-plants; the habitus of a *Juncus*, for example, is distinctly Xerophilous. Among the so-called irritable plants the *Mimosa* is one of the most striking. It has been conjectured that its movements form a protection against the injuries caused by hail. But in the regions where *Mimosa* grows, it either does not hail at all, or only quite exceptionally. The tendency to sleep on the part of the leaves has been pointed out as a protection against the radiation of heat. But very many tropical plants exhibit this tendency to sleep, and in those parts of the world there can scarcely be a question of the need of protection in this respect.

Insectivoræ have recently occupied a considerable share of attention,² not only from a morphological but also from a physiological point of view. As regards the latter I will only mention the fact that *Sarracenia* and *Cephalotus* do not possess a digesting ferment or enzyme, but the *Cephalotus* secretes into its pitcher a substance which works antiseptically. It was also recently maintained—in contradiction to the statements of Hooker, Darwin, Rees, Vines and others—that in the case of *Drosera*, *Nepenthes* and *Pinguicula* no actual digestion obtains, but that the solution

¹ For striking instances of this, cf. Pflanzenbiol. Schilderungen, ii., p. 3.

² Pflanzenbiol. Schilderungen, ii. theil.

of the animal body took place by means of bacteria. These statements, which have been made by Tischutkin, Dubois and others, are based, however, on an insufficient knowledge of the conditions of life of those plants, as has been shown in another place. On the other hand, it has lately been proved that there is a systematic relationship existing in the case of some chlorophyll Thallophytes, which are destitute of chlorophyll. Kamienski first drew attention to the fact that the roots of a plant which lives as a saprophyte, *Monotropa hypopitys*, are so closely invested by fungal hyphæ that the nutriment is only absorbed by means of this sheath. Since then there have been found fungi either on or in the roots of all saprophytes, as also in a number of plants (Cupuliferæ, etc.), which were hitherto not regarded as such.¹

The part which the fungus plays, particularly in the last-mentioned cases, is, in spite of all contrary assertions, still doubtful, and we cannot yet affirm that the root-tubercles of the Leguminosas and their bacteroids, which have been so carefully studied within recent years, have been quite satisfactorily explained. It seems clear that the formation of the little tubercles occurs as a consequence of the influence exercised by some bacterium, and that the organisms subsequently assume the Involution form known as "bacteroids," which are bodies rich in nitrogen, and capable of being digested by the plant.

A treatise by Stahl² awakened particular interest in the means of protection of plants against the lower animals, especially snails, which play an important part in our own country as enemies of vegetation. Many plants are protected from them, partly chemically and partly mechanically, *i.e.*, by the constituent parts of their tissue, which render them unpalatable to snails (tannin, acids, bitter substances, ethereal oils and oily bodies as in the liver-wort, or by bristly hairs, calcareous or silica cell-

¹ Cf. the detailed account in Frank, *Lehrbuch der Botanik*.

² E. Stahl, *cf. Pflanzen u. Schnecken, eine biologische Untersuchung über die Schutzmittel der Pflanzen gegen Schneckenfrass*, Jena, 1888.

walls, mucilage, etc., raphides and other crystals of calcium oxalate).

The physical adaptations appear in the mechanical construction of the tissues in the form of the plant organs (leaves, roots, etc.), and in active response to stimulus. As regards the adaptation of the tissues, the progress made in this sphere has not been very extensive since Haberlandt brought together, in his *Physiologische Pflanzenanatomie*, the results which had been arrived at up to that date. It may, however, be worth while to refer to the researches on the importance of intercellular spaces in marsh and aquatic plants. They have been regarded until recently as air-reservoirs, which provide the plants with an internal atmosphere. But, at the same time, it remained quite incomprehensible why the parts of marsh plants which did not come in contact with the water or the damp soil should contain large intercellular spaces. I have endeavoured (in the work to which I have frequently alluded) to point out that it is here principally a question of providing the submerged parts with oxygen, of which there is a proportionately smaller quantity in water than in air. Oxygen is separated during the assimilation on the part of the green portions, it reaches the intercellular spaces, and can so easily be distributed, as the intercellular spaces represent either a connected system, or else the diaphragms which separate them are easily penetrated by gases. If the tissue containing the numerous intercellular spaces owes its origin to the action of a cork-cambium, we have the *Aerenchyma*, which clothes the submerged parts of certain plants in a thick, white covering; and the light, air-containing wood of some plants fulfils exactly the same function, and it was formerly believed to serve as "swimming-wood". These adaptive modifications are entirely wanting among the greater part of our native plants.

I should exceed the space allotted to me if I were to attempt to even mention the most important results of the researches on the physical adaptation of the *external* organs of plants. So many valuable contributions have,

in this field especially, been added to our store of knowledge that the enumeration of a few cases must suffice, *e.g.*, Epiphytes,¹ succulents,² mangrove-vegetation,³ aquatic plants,⁴ climbing plants,⁵ etc.

I will now briefly review the various theories of adaptation which have been put forward. This can only be done briefly, as a more detailed account would take up a whole book.

The best known and most familiar theory of adaptation is that of Darwin. In the main his theory is one of "the survival of the fittest". He attaches a certain, though somewhat slight, importance to the conditions of life, and to the effects of the use or disuse of organs. Hence it is clear, however, that, regarded from this point of view, the question is not so much one of how plants *become* adapted, as the selection of those which *have become* adapted. For adaptation clearly means that the organs possess the faculty of changing their structure and form by the influence of external conditions. That, within certain limits, this power is inherent in plants, nobody doubts, but the question is, whether organic conditions which have become *hereditary* can originate in this way. Nägeli's⁶ theory of adaptation distinguishes between two kinds of changes which take place under external influences: temporary changes, which only last as long as their cause, and lasting changes, which con-

¹ Schimper, die epiphytische Vegetation Americas (*Bot. Mittheil. aus den Tropen*), Goebel, Pflanzenbiol, Schilderungen.

² Goebel, *ibid.*

³ Goebel *ibid.*, Schimper, *l. c.*; Karsten, Die mangrove vegetation (*Bibliotheca botanica*).

⁴ Goebel, Schilderungen, ii.; Schenk, Die Biologie der Wassergewächse, Bonn, 1887.

⁵ Treub, Sur une nouvelle catégorie de plantes grimpantes, and Observations sur les plantes grimpantes du jardin botanique de Buitenzorg, *Annales du j. b. de Buitenzorg*, vol. iii. Schenk, Lianen, in *Botan. Mittheil. a. d. Tropen*, iii., iv.

⁶ Nägeli, Mechanische Physiologische Theorie der Abstammungslehre, 1884.

tinue after the cause has ceased to operate. Thus changes of climate or nutrition are followed by immediate visible results, but the results are but temporary, and disappear when their causes are removed. He quotes the alpine *Hieracia* as an example, which in the plains immediately begin to produce numerous leaves and blossoms and assume a luxuriant habit, very different from the original stunted plant, with its miserable and starved-looking organs.

In my opinion the external conditions, which produce temporary changes, act in a twofold way: they can prevent the appearance (or occurrence) of certain organs, or they can influence the growth of those organs which are originating in the special meristem. The first-named effect becomes possible when the development of a plant is not already definitely predestined from its first origin, but is determined during the course of development. The constitution of the individual Protoplasm certainly gives *direction* to the course of development, but the actual course followed depends on certain external factors. A few examples will serve to explain this. Every one is familiar with the fact that our *Sagittarias* (and also a few other monocotyledons, aquatic and marsh plants) produce two kinds of leaves, *viz.*, ribbon-shaped, submerged leaves and sagittate ones, which rise above the water-surface; the first-named forms occur during early development when the plant grows in its usual state in shallow water; they represent, however, the only kind of leaf which is formed when the plants grow in deep or rapidly-flowing water. What could be more simple than to assume that the one leaf-formation is an adaptation to an aquatic habit, the other to an aërial one? And yet this assumption would not be correct. For my own researches have proved that the ribbon-shaped leaves represent the original ones which are so widely diffused among the Monocotyledons and that the sagittate ones are clearly only a further development of the same. The ribbon-shaped leaves occur also when the plant exists in the air from the beginning of its life; they have first to

manufacture the substances which are requisite for the development of the sagittate leaves. That the latter do not occur in deep or rapid water is not due to the *water*, but to the diminution of light. I succeeded in rearing *Sagittaria* plants with leaves sixty cm. long and of ribbon shape, and deep green colour, and to limit the plant to that construction of leaf mainly by exposing it to less light. As the *Sagittaria* is increased by means of tubers, one could continue to rear them, doubtless, for generations in this form, which differs so widely from the normal. In the same manner moss-protonema, as such, can be cultivated for years; moss plants only begin to appear on them when they are exposed to light of a certain sufficient intensity.

Among the *Opuntias* there are some species which possess cylindrical shoots, others again in which they are quite flattened; the former are clearly the more primitive, and if the more flattened stemmed *Opuntias* are exposed to less intense light, they become cylindrical. In every case the apex is cylindrical, but in many kinds it soon gives rise to a flattened axis under the influence of light; but if the transforming agency is removed, the original nature of the shoot becomes manifest. Similar results were obtained with *Mühlhenbeckia platyclada* and some other plants. Other agencies can exert an influence analogous to that effected by light. One of our most common liver-worts, *Frullania*, has helmet-shaped pendants to its leaves, the "auriculæ," and they are organs which are able to retain water by capillary attraction. If the plant is cultivated under damp conditions, the auricle portion of the leaves develops as ordinary leaf-lobes; a similar function is performed by the perforated, empty cells in the leaves of the *Sphagnum*. Some *Sphagnum* species, however, only possess ordinary chlorophyll-containing cells like other mosses when they grow in a submerged condition. On the leaves of *Polytrichum* there are on the mid-rib closely-packed lamellæ consisting of chlorophyll containing cells which retain water in between them. It is possible to effect the suppression of those lamellæ also when the plant is cultivated in damp conditions.

As regards the second kind of influence—that of growth—it will be well to remember in the first place the division of the different phases of growth, which Sachs¹ has made. He distinguishes two periods in the development of the organs :—

I. Morphological period—

- (1) Origin of the organs according to number and position.
- (2) Embryonic growth of the organs, morphological configuration, position in the bud.

II. Physiological-biological period—

- (3) Extension of the organs up to reaching their definitive size.
- (4) Internal development of the tissue, and the maturation of the plant organs.

The influence of external factors concerns only the physiological-biological periods, but its influence may, nevertheless, be a very striking one. And here it will be well to quote a few examples.

The characteristic habits of many Alpine plants are generally known ; the low growth of the shoot-axis, and the relatively energetic development of the subterranean parts. Gaston Bonnier² investigated the effect of an elevated Alpine position (more than 2000 metres) on a number of plants inhabiting the lowlands. Out of 203 of the plants examined, 123 remained living in the high regions, and they exhibited the following changes : the whole plant was smaller, and its stems grew nearer the ground ; some had undergone such striking changes that they could only with difficulty be recognised, such as the *Helianthus tuberosus*, which had developed on the ground a rosette densely clothed with hairs, instead of the ordinary elongated shoot. The leaves remained smaller and thicker in proportion to the surface, and they were of a deeper green than those from lowland-grown specimens, and some even acquired a brownish-red colouration. The subterranean parts

¹ *Flora*, 1893, p. 377.

² *Revue de botanique*, ii. 513.

became more strongly developed in proportion to those parts above ground, and some species, which are annuals in the plains, became perennials at the higher elevations. These "transitory changes" answer, in general, to the characteristic, *hereditary* peculiarities of Alpine plants. Analogous instances might be quoted, particularly in the cases of aquatic plants, and in still greater numbers. But I would prefer to point out a few cases of the reaction of tissues to the requirements of their surroundings.

It is known that transpiration conditions affect the thickness of the outer walls of the epidermal cells, together with the cuticle, and even the development of the palisade parenchyma is influenced by similar conditions, and of the truth of this Stahl's *Licht-und Schatten-Blätter* are an example.

As a further fact of interest it may be mentioned that the dimensions of the intercellular spaces increase in damp air or in water. Hegler has recently described a particularly striking instance of the effect of the environment on tissue-development. If one exposes the growing parts of a plant to a mechanical strain, the existing mechanical elements increase in thickness and number, and *even tissues, which were lacking hitherto, may be formed*. The hypocotyl of the seedlings of *Helianthus annuus*, which broke under a weight of 160 grams, was able to bear 250 grams after two days, and in a few days 400 grams. In the leaf-stalks of the *Helleborus niger* there are normally no bast-fibres, but on introducing a mechanical stretching or pulling strain they appear and form effective strands round the phloëm. The faculty of forming these tissues was, therefore, latent in those leaf-stalks, but it was only rendered evident in consequence of the influence exercised by the mechanical strain. And this leads to the discussion of the influences which, according to Nägeli, produce lasting and hereditary changes. This is said to take place by means of forces which exert their influence for very long periods, and for a long series of generations, and in this way actually alter the construction of the idioplasm. The extent of the direct influence cannot be proved, but can only be deduced from general considerations. According to Nägeli evaporation acted as a stimulus,

which caused the production of cork; as the result of the effects of stresses and strains the mechanical cells were developed, the corolla is supposed to have been evolved from the stamens, as the direct result of the stimulus due to the continual irritation and damage caused by insects in their search after pollen or honey. Disregarding this last hypothesis, which can only be designated as a fantastic picture, we may inquire whether the marked distinction which Nägeli drew between transitory and permanent influences can really be proved to exist. The difference might lie in the different possibilities of response evinced by different plants, just as a soft rod of iron which is magnetised soon after loses the magnetism, whereas a steel rod retains it.¹ Doubtless the theory of direct influence, which in a certain sense goes back to Lamarck, has much that is very attractive. It would also explain far more easily why organs, which have become useless, so frequently become reduced, and I should wish—in opposing Nägeli's views—to point especially to the study of the transitory influences, from which we should derive further valuable hints.

We must not, however, forget that such adaptations are only relative and conditioned by the organisation of the plants in question. In the Darwinian theory of adaptation, organisation and adaptation are coincident, as the former arises from the gradual accumulation of useful alterations. But even on this explanation a series of organic conditions remains incomprehensible, especially the division of labour which has really nothing to do with adaptation. In a genus of Hepaticæ, *Symphyogyna*, there are species, the vegetation body of which forms a Thallus, and others in which it is present as a leafy shoot.

It is inconceivable why the leaf-formation should be more useful than the Thallus-formation. And the same is true in the case of *Fucus* and *Sargassum*. According to the

¹ The aerial roots of some orchids become flattened and change their structure on the side exposed to the light, and this does not occur on the shady side. This dorsiventrality in some formations (*Sarcanthus*, *Phalænopsis*) is directly due to the operation of light. In others (*Aeranthus funalis*) it is hereditary, and independent of light.

opinion of Nägeli, Sachs and myself, the selection cannot play the part ascribed to it by Darwin. Without it, according to Darwin's theory, a perfecting of the organisation could not take place; it is, so to speak, an active force. But in our opinion it only removes those organisms which are least fitted for existence, and if it ceased to operate there would still remain the same variety of forms which we now see, only vastly increased by those developments which had perished in the struggle for existence. I have endeavoured to show in my *Pflanzenbiologische Schilderungen* that we know of a similar case in a certain group of plants. The Podostemons are aquatics, which exist under peculiar conditions. For they only occur in rapidly-flowing waters, especially rapids and waterfalls. Their peculiar habitat has stamped on them characteristic marks of adaptation, but, in spite of this, they possess an astonishing variety of structure. This fact is explicable on the ground that "selection" scarcely affects them—at any rate, much less than is the case with land-plants; with them transpiration, conditions of gravity, animal enemies, and the competition with other plants, are all realities which have to be reckoned with. It is very much the same with sea-weeds; it would scarcely be possible to refer the variety of their forms to selection as an adequate explanation of their existence. We may almost say, moreover, arrangements of such—unnecessary—complication as are connected with the fertilisation of orchids cannot be explained on the ground of selection alone, the modest blossoms of our common weeds are better "adapted," and no doubt the dusting with pollen is carried on more surely than is the case with the marvellously complex flowers of orchids.

But all these questions can hardly be more than touched on here. The endless field of the science of adaptation has yet to be cultivated. May the English botanists take a large share in this! For they possess in the rich treasures of plants at Kew and in the English colonies a richer and more adequate material for such researches than any one else in the world.

K. GOEBEL.

Corrections to Professor Howes' Article, "On the Present Outlook of Vertebrate Morphology," which appeared in the first number of this Review.

Page 73, line 26, *for* "aquatic" *read* "marine".

" 73, footnote, *for* "entwicklungsgeschz" *read* "entwicklungsgeschl".

" 74, line 10, *for* "dalamination" *read* "delamination".

" 74, " 11, *for* "Ophinroids" *read* "Ophiuroids".

" 74, footnote, *for* "Try onidae" *read* "Trygonidae".

" 74, " *for* "Amphipuons" *read* "Amphipnous".

" 74, " *for* "Sarrohanchus" *read* "Succobranchus".

" 75, reference 21, transpose to after "European area".

" 76, line 17, *for* "Marsipohanchii" *read* "Marsipobranchii".

" 76, " 31, *for* "Froriep's" *read* "Froriep's".

" 78, last line, *for* "Sluirteri" *read* "Sluiteri".

" 84, line 12, *for* "archipterygial" *read* "archipterygial".

" 84, " 14, *for* "archipterygium" *read* "archipterygium".

" 86, " 12, *for* "additions" *read* "addition".

" 89, last line, *before* "Morph. Arbeiten" *insert* "Schwalbe's".

" 90, lines 4 and 5 from bottom, *for* "bonw e. d. ontwick g." *read* "houw e. d. ontwicklg".

[NOTE.—The above corrections have been rendered necessary owing to the difficulties connected with the punctual appearance of the first number and to the fact that the MS. was received late.—Ed.]